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Regional Recruitment Dynamics and Seasonal Ecology of Juvenile Bluefish (Pomatomus Saltatrix)

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REGIONAL RECRUITMENT DYNAMICS AND SEASONAL ECOLOGY OF

JUVENILE BLUEFISH (*POMATOMUS SALTATRIX*)

A Dissertation Presented

by

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DEDICATION

To my beloved parents

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ABSTRACT

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Recruitment in fishes, defined as the survival of a cohort through the first year of life, can be highly variable and affected by small changes in biological and physical factors. Much of the historical focus into the sources of recruitment variability has concentrated on the larval stage, but recent attention has shifted to the relatively longer juvenile period. Spawning behavior that results in the production of multiple cohorts over time and space within a year-class may dampen recruitment variability by decreasing natural mortality risk. The bluefish (*Pomatomus saltatrix*) is a migratory marine species that produces multiple cohorts of offspring during annual spawning migrations. Juvenile bluefish are among the fastest growing fish in the ocean. Consequently, bluefish is one of the few species that both mature and enter the fishery shortly after its first birthday, so recruitment success may be particularly critical in determining year-class strength. The following dissertation explores the factors that influence recruitment potential of bluefish. The first chapter provides a brief history of the study of recruitment in fisheries science and an introduction to bluefish life history. Chapter two investigates the interaction between the juvenile bluefish cohorts in the Hudson River estuary prior to the autumn migration. Chapter three presents the discovery of the northern Florida coastal ocean as an essential habitat to juvenile bluefish during the winter. The final chapter provides a summary of the main conclusions from chapters two and three.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

A GENERAL INTRODUCTION TO FISHERIES RECRUITMENT SCIENCE

AND THE REGIONAL RECRUITMENT DYNAMICS OF JUVENILE

BLUEFISH

1.1 Recruitment: a brief early life history

1.1.1 Hjort's legacy and the emphasis on the larval stage

In the early days of fisheries science, the study of fish populations focused largely on the

effects of fishing on the growth, reproduction and mortality of adults (Cowan and Shaw

2002). During the early twentieth century, fisheries biologists began to understand that

assessing adult vital rates did not adequately explain the great inter-annual variability in

population size. The Norwegian fisheries scientist Johan Hjort first suggested that the

earliest life history stages of fish determined year-class strength. Hjort (1914) observed

near 100% mortality of the egg-to-larval stages of several North Sea fishes and

hypothesized that the time to reach the first-feeding stage was a critical period for larval

fish survival, and ultimately determined the strength of the corresponding year-class.

From this notion began a revolution in fisheries research which emphasized the

importance of understanding the factors that influence the variability in first year

survival, otherwise known as recruitment. Thereafter, the term recruitment has been used

to represent a variety of fish life history stages or events (e.g., settlement timing of

demersal fishes, age or size at 50% maturity, size or age at entry into a fishery). For the

purposes of this thesis, the term recruitment will hereafter represent the survival of a

cohort of juveniles to age-1 and the factors that affect survival (recruitment dynamics).

Hjort (1928) postulated that recruitment potential depended upon successful transport of eggs and larvae from spawning areas to nursery areas ('aberrant drift' or 'offshore transport') and whether enough food was available in the nursery areas during a defined 'critical period' of early life from endogenous to exogenous feeding. Under a food limited scenario or unfavorable oceanographic conditions during transport, larvae wouldn't find enough food and starve, but survival would be high when prey were abundant or larvae encountered a good hydrodynamic environment, leading to the concept of recruitment variability and its influence on year-class strength. Although larval survival has been broadly associated with high prey levels (Cushing 1990), there is little evidence to suggest that mortality is concentrated at the earliest larval stages (May 1974) and the limited focus of the critical period hypothesis has since been shown to be misleading (Houde 2008). Nevertheless, these two concepts together formed the foundation of the study of recruitment in fisheries for which subsequent hypotheses were developed to address the recruitment 'problem' in fisheries research.

For decades after Hjort's 'critical period' concept, investigations of the causes of recruitment variability progressed slowly and the variability was treated as noise in assessments of fish populations (Sale 1990). Cushing (1972, 1975) removed the 'critical period' restriction of Hjort's two-stage hypothesis, suggesting that recruitment potential depended on larval encounter rates with plankton over a duration that extended almost the entire larval stage. Under this 'match-mismatch' hypothesis, fish larvae would either be variably 'matched' with the abundant food or will miss peak production (mismatch)

and starve, resulting in a good or bad recruitment year respectively. Multiple

experimental simulations have demonstrated that first feeding and post-first feeding

larvae are susceptible to starvation (Miller et al. 1988; Pederson et al. 1990). However,

the support for a relationship between prey quantity during the early larval period and

recruitment from the initial field-based studies proved inconclusive. In nature, fish

spawning is known to occur over relatively constant time periods and at geographically

similar locations from year to year, but the timing of the production cycle exhibits

considerable inter-annual variability depending on physical processes (Cushing 1975).

Hence, the efforts to understand recruitment dynamics shifted to focus on the relationship

between density independent factors and larval survival, incorporating the association

between physical oceanographic features (e.g., upwelling and downwelling, plumes,

fronts, gyres, eddies etc.) and the magnitude of the production cycle (Lasker 1978;

Cushing 1982).

Rooted in the construct of Hjort's 'Aberrant Drift' or 'Offshore Transport' concept, Sette

(1943) concluded that the poor year-classes of Atlantic mackerel observed during some

years resulted from variable advection of larvae due to variable drift and wind. These

early observations lead to the development of the 'Member-Vagrant' hypothesis (Iles and

Sinclair 1982; Sinclair and Tremblay 1984), which held that spawning and subsequent

retention of larvae at times and in areas with favorable oceanographic conditions were

more determinant of recruitment success than prey availability. Calm years resulted in

strong year-classes, while stochastic climatic events including storms were shown to

carry eggs and larvae away from nursery areas, resulting in poor recruitment (Miller and

Kendall 2009). Pelagic fishes including Atlantic herring that spawn in association with physical conditions rather than peak secondary production were characterized by this hypothesis (Sinclair 1988). The take-home message of this hypothesis was that biotic interactions were less important than abiotic conditions at the location of spawning that drove year-class strength.

It became apparent to fisheries professionals that starvation during first-feeding was not the sole determinant of larval survival and successful recruitment, but the likely fate of a large proportion of the eggs and larvae was to die from predation. Although few studies have directly quantified the contribution of predation to recruitment, Ware (1975) showed that the match or mismatch between fish larvae and their prey directly affects growth, resulting in more or less time spent in the early life stages most vulnerable to predation. Consequently, as fish grow through these vulnerable life stages, they pass through fewer predator fields resulting in lower predation mortality. Houde (1987) postulated that a modest reduction in larval growth rate and an older age metamorphosis could result in orders of magnitude higher predation mortality and ultimately a weak year-class. The concept of small larvae remaining more vulnerable to predation for a longer duration than large conspecifics came to be known as the 'stage-duration' hypothesis (Cushing 1975), implying that large size and fast growth increase recruitment success and has been demonstrated by Hare and Cowen (1997). This hypothesis has been further supported by Pepin and Myers (1991) who found that recruitment success of twenty-one different species was positively correlated with size at hatching and size at metamorphosis, which the authors equated to the duration of the larval stage. The 'stage-duration' hypothesis

was extended by Shepherd and Cushing (1980) to include growth rate, such that predation of fish larvae should decline with increasing larval size. This extension resulted in the development of the 'growth-mortality' theory (Miller and Kendall 2009), wherein larval survival was proposed to be directly related to growth. Together, these hypotheses assumed that mortality from starvation and predation did not act independently and represented a novel way to view the dynamics of recruitment variability, forming the foundation of the recruitment science discipline from which originated a substantial body of research efforts.

The 'bigger is better' hypothesis (Miller et al. 1988; Bailey and Houde 1989) incorporated the influence of the aforementioned concepts on recruitment, such that larger hatchlings and faster growing larvae ultimately attain a larger body size at a given age, and thus should be less vulnerable to predation. Although this hypothesis is supported by number of field and experimental investigations, it only applied to the larval stage. Moreover, this concept was antithetical to other concepts of the time, including optimal foraging theory, which postulated that predators should select for larger larval fish prey to maximize the energetic benefit to the foraging cost tradeoff (Stephen and Krebs 1986). Leggett and Deblois (1994) suggested that disproportional predation on larger individuals within a population comprised of multiple cohorts could negate any survival advantage arising from favorable feeding conditions experienced by larvae at earlier stages, and this was supported by Bertram (1993) who showed that predation was highest during the later larval stages of several flatfish species.

Perhaps the single most important breakthrough advancing research on the early life history of fishes was the discovery that daily increments are laid down in otoliths (Pannella 1971). This revolutionary breakthrough in fisheries science provided the ability to confidently and accurately determine the age of young fish and estimate growth rates during early life. More recent technological advances and increased computational power have led to the development of complex statistical models that have coupled the tropho- and hydro-dynamics of oceanographic conditions and the early-life stages of fishes (Houde 2008), and demonstrated how recruitment variability could be produced (Hinckley et al. 2001; Werner et al. 2001; Mullon et al. 2002; Bartsch and Coombs 2004). This progress in recruitment science has contributed to a better understanding of the causes of recruitment variability.

1.1.2 The importance of the juvenile stage

The preceding efforts to understand recruitment dynamics operated on the assumption that year-class strength (and recruitment) in marine fishes was regulated by feeding success and/or predation during the larval stages. However, support for this idea remains uncertain from a paucity of direct correlations between the abundance of these life stages and year-class strength (May 1984; Smith 1985; Peterman et al. 1988; Wooster and Bailey 1989; Taggart and Frank 1990). Gulland (1965) perhaps first hypothesized coarse control of recruitment during the larval stages and fine control during the juvenile period. Fishes exhibit a range of metamorphoses from the larval to the juvenile stages that are characterized by changes in anatomy, habitat and behavior which can considerably influence survival rates. Sissenwine (1984) proposed that predation during the juvenile

stage could contribute a significant proportion to the total pre-recruit mortality in some species. Moreover, Leggett (1986) pointed to the significance of feeding and predation processes at finer scales during the period of juvenile development. Thereafter, several investigators showed that recruitment potential did not correlate with the egg and larval abundance, but with mortality during some time after these stages (Butler 1991; Watanabe et al. 1995, 2002, Nash and Dickey-Collas 2005). For example, the National Oceanographic and Atmospheric Administration (NOAA) which conducts the fisheries-oceanography coordinated investigations (FOCI) of the recruitment dynamics of fishes in Shelikof Strait and the Gulf of Alaska, concluded that little variation in mortality occurs during the earliest life history stages (Miller and Kendall 2009).

A negative feedback may exist in the 'growth-mortality' theory, wherein a 'match' year leads to a strong year-class, but not without density dependent reduction in growth and potentially increased mortality at some point during early life stage(s). The question then becomes, when do these density dependent growth effects occur and to what extent? Mackenzie et al. (1990) showed that larval feeding rates in nature are normally at or near satiation levels, and largely independent of food density. In addition to the biological metamorphosis associated with the transition from the larval to the juvenile stage, the feeding ecology of many species also changes during this period. Rothschild (1986) concluded that a density-dependent reduction in growth rate during the early life stages could have substantial impact on recruitment dynamics. However, relatively little observational support exists for strong density dependence at the egg and larval stages (Houde 2008).

Environmental conditions that lead to fast growth during the larval stages could result in the inability of predators to functionally or numerically respond fast enough to reduce larval abundance, creating a lag in predation and subsequent delay in the density dependent response until the juvenile stage. There is strong evidence for the effects of density dependency during the juvenile stage on recruitment dynamics (Cowan et al. 2000; Doherty 2002; Shoji and Tanaka 2007). Hence, the implications of high larval survival on recruitment success could be invalidated by reduced survival in the later stages (Myers and Cadigan 1993). Size-selective predation of smaller juveniles which could act in a compensatory way to reduce recruitment and juvenile mortality sufficient enough to cause fluctuations in recruitment have been demonstrated in a number of fish populations (Myers and Barrowman 1994). These processes, which operate during the post-larval stages, may be strong enough to moderate if not regulate recruitment in fish populations (Bailey 1994). Population regulation is an expression of the compensatory ability that generally reduces variability and tends to stabilize recruitment variability and much of the compensation may occur in the juvenile stage.

We now generally acknowledge that recruitment is a highly variable process that has important implications for fish populations. It is also clear that the mortality rate of young fish decreases through successive life history stages from the egg to age-1 due to the differences in the magnitude of stage-specific abundance, but is dependent on abiotic and biotic conditions specific to each stage (Houde 1997). This view recognizes that the factors affecting survival (e.g., feeding intensity, growth, condition) change as fish

transition from one stage to another, but these changes are likely specific to each stage and under some degree of density dependent regulation. Therefore, it is important to evaluate the stage-specific effects of these factors on recruitment, for it will be during one or more of these stages in the first year of life that year-class size is determined. Without constant and intensive monitoring of the early-life stages and the factors that affect survival, accurate recruitment forecasts will remain an elusive goal.

1.2 Recruitment dynamics and seasonal ecology of juvenile bluefish

1.2.1 Spawning behavior and early life history along the U.S. Atlantic coast

Bluefish (*Pomatomus saltatrix*) is a highly migratory pelagic species found worldwide in sub-tropical, and temperate waters except for the eastern Pacific (Juanes et al. 1996). Along the U.S. east coast, adult bluefish occur seasonally in the western Atlantic Ocean from Maine to Florida (Kendall and Walford 1979), migrating in loosely aggregated schools of similarly sized individuals (Olla and Stoudholme 1972). The timing of bluefish migrations appear to be largely regulated by water temperature (Hare and Cowen 1996). Generally, concomitant with decreasing autumn water temperatures, bluefish emigrate from middle Atlantic bight (MAB) estuaries and coastal waters and begin a southerly migration towards the warmer waters of the South Atlantic Bight (SAB) to spend the winter (Buckel et al. 1999a; Munch and Conover 2000). Although the exact temporal and spatial patterns of bluefish spawning remain uncertain, at least two primary events occur during these migrations in the spring and summer in continental shelf waters. Spring-spawning typically occurs in the SAB from Cape Hatteras, North Carolina to Cape Canaveral, Florida (March – May), and summer-spawning occurs from

June to August along the MAB from Cape Hatteras to Cape Cod, Massachusetts (Hare and Cowen 1996). Two principal cohorts of offspring (spring- and summer-spawned) are produced as a result of this temporal spawning behavior.

Spring- and summer-spawned bluefish eggs hatch approximately two days after spawning and develop into post-yolk sac larvae after another one to two days (Deuel et al. 1966). The larvae are passively transported north in the Gulf Stream (spring-spawned cohort) or in the cross-shelf current (summer-spawned cohort) and both cohorts subsequently transform into pelagic juveniles after three to four weeks (Juanes et al. 1996). Juvenile bluefish remain in shelf waters for two to six weeks before actively entering the estuarine and nearshore coastal ocean nursery areas of the MAB (Hare and Cowen 1996; Able and Fahay 1998). Upon entry into these nursery areas juvenile bluefish become piscivorous and exhibit an increase in growth rate, due in part to a shift from invertebrate prey to piscine prey (Juanes and Conover 1994). After spending the summer in MAB waters, both cohorts of juvenile bluefish migrate either offshore or southward in autumn to overwinter along the deep continental slope or the warm waters of the southern SAB.

The relative contribution of the spring- and summer-spawned cohorts to the western Atlantic population varies and has been the topic of some debate (Juanes et al. 1996; Hare and Cowen 1996; Munch and Conover 2000; Conover et al. 2003). In the 1950s the relative abundance of spring-and summer-spawned cohorts was nearly equal (Lassiter 1962). From 1973-1995 spring-spawned bluefish dominated the cohort structure of juvenile bluefish inhabiting the MAB (Munch and Conover 2000). An apparent shift in

recruitment has favored the summer-spawned cohort since the mid-1990's, but the

summer-spawned cohort does not appear to be contributing proportionally beyond the

juvenile stage (Conover et al. 2003). Hence, the cohort structure of juvenile bluefish

may be more complex than previously recognized and could have implications for

recruitment success.

The 'bigger-is-better' and 'growth-rate' elements of the 'growth-mortality' theory apply

to bluefish larvae due to the relationship between larval survival and size and growth, but

directional selection influences size and growth during the entire larval stage, indicating

that no specific larval stage is critical to survival (Hare and Cowen 1997). Moreover, the

transformation time or pre-juvenile period from the larval to the juvenile stage is

relatively short for bluefish when compared to other pelagic fishes (Miller and Kendall

2009), while the remainder of the first year of life is spent in the juvenile stage.

Consequently, the requirements of fast growth and energy storage during summer and

early autumn to survive the long-range autumn migration, as well as the need to find

adequate habitat during winter means that it may be the pelagic and migratory juvenile

stage which drives recruitment potential in bluefish.

1.2.2 Purpose and need

In the United States, bluefish support an important commercial and recreational fishery

with recently reported annual landings over 3,000 and 7,000 metric tons respectively

(Shepherd and Nieland 2010). Bluefish is currently being managed under an interstate

management plan, which relies on the contribution of juvenile and adult abundance

indices from multiple state agencies and the National Marine Fisheries Service (NMFS).

Concern over persistent northwest Atlantic bluefish stock biomass estimates below the

biomass target level after years of reductions in commercial and recreational catches,

coupled with recently low estimates of recruitment have prompted the Atlantic States

Marine Fisheries Commission (ASFMC) to establish research needs for bluefish that

support a coastwide bluefish stock assessment with emphasis on the examination of

recruitment dynamics.

1.2.3 A prelude to chapter 2: the recruitment dynamics of juvenile bluefish in preparation for the autumn migration in the Hudson River estuary, New York.

The Hudson River in southeastern New York is important to many fishes during all or

part of their life cycle. The estuarine portion of the Hudson River is composed of a

diverse assemblage of marine, freshwater and estuarine fishes including bluefish (Beebe

and Savidge 1988). The spring-and summer-spawned cohorts of juvenile bluefish use the

lower Hudson River estuary (HRE) extensively in their first year of life and have been

historically abundant in the estuary during summer and early autumn (Juanes et al. 1993).

Even as juveniles, bluefish are top trophic-level predators in the lower HRE and play an

important role in structuring ecosystem level ecological processes (Scharf et al. 2006).

Unfortunately, the fish community of the lower HRE has been declining in diversity for

over three decades (Hurst et al. 2004). Seaby and Henderson (2008) suggested that the

Hudson River fish community is also becoming increasingly unstable, showing that 10 of

the 13 species examined have declined in abundance since 1985, citing elevated water

temperature, decreasing dissolved oxygen levels, and invasive species as possible explanations for the observed trends. Moreover, several of the species declining in abundance are known prey of juvenile bluefish. Heimbuch et al. (2008) noted that since 1990, the relative abundance of juvenile blueback herring (*Alosa aestivalis*), alewife (*Alosa pseudoharengus*), Atlantic tomcod (*Microgadus tomcod*) and white perch (*Morone americana*) in the Hudson River have declined by over 50%. Schultz et al. (2006) reported a 10-fold decline in abundance of bay anchovy *Anchoa mitchilli* in the HRE since the late 1980's. Bay anchovy is an important forage fish for both cohorts of juvenile bluefish, and has been shown to represent the dominant prey base for the summer-spawned cohort (Juanes et al. 1993, Scharf et al. 2002). Concomitant with the declines in forage fish abundances, the New York State Department of Environmental Conservation (NYSDEC) catch-per-effort (CPE) of juvenile bluefish since 2000 has declined by nearly half of the CPE during the preceding two decades (Stormer unpublished data).

Although previous studies have examined the diet composition of juvenile bluefish during summer residency in the HRE (Juanes et al. 1993; Buckel and Conover 1997), its feeding ecology has not been investigated since the recent concern over declining forage fish abundances, reduced juvenile indices and apparent shift in cohort structure. Simulation modeling of prey abundance and time of entry to the estuary suggested that even modest fluctuations in prey densities could generate considerable variation in prey consumption and growth realized by summer-spawned bluefish, but the spring-spawned cohort was less affected by prey-specific abundance and timing (Scharf et al. 2006). The

apparent shift in cohort structure and the changing fish community of the HRE may be affecting the recruitment dynamics of juvenile bluefish prior to the autumn migration and warrants investigation.

1.2.4 A prelude to Chapter 3: the overwinter recruitment dynamics of juvenile in the northern Florida coastal ocean.

Scientists, fisheries managers and industry professionals at all levels have agreed that healthy and abundant fish habitat is essential in protecting and enhancing commercially and recreationally important fish populations. For juvenile fish, quality nursery habitat promotes rapid growth while offering protection against predation (Ross 2003). Habitat alteration and degradation has been associated with the decline of many coastal marine fishes (Caddy 2007). Natural mortality is the primary source of mortality during the juvenile stage of most fishes and is, in part, habitat-dependent (Houde 1987). Consequently, successful recruitment in many commercially and recreationally important fishes is largely affected by the quality and quantity of nursery habitat (Juanes 2007). This point is underscored by the Magnuson Fisheries Conservation and Management Act, which lists provisions that address the need for proper identification and protection of essential fish habitat (EFH) and the National Marine Fisheries Service (NMFS) recently implemented the EFH Initiative to define important fish habitats in an effort to improve habitat assessments in fisheries management plans.

For fishes that use coastal habitats during the juvenile life history stage, the nearshore coastal ocean functions similar to estuaries in providing nursery habitat (Lasiak 1986;

Robertson and Lenanton 1984). Nearshore oceanic waters provide refugia and food for developing juveniles during this critical life stage (Lasiak 1986). However, much of the attention paid to coastal community dynamics has concentrated on the surf zone and estuaries while relatively little information exists addressing nearshore continental shelf habitat. Spatial trends have been observed in nearshore juvenile fish communities, increasing in species richness with depth from the surf zone to shallow shelf habitat (Layman 2000). Due to the dynamic nature of coastal processes, Wilbur et al. (2003) suggested more intense sampling of these systems over greater temporal and spatial scales to reliably assess the role of non-estuarine coastal areas as nursery habitat for juvenile fishes.

Essential fish habitat classification is inadequately known for juvenile bluefish (Fahay et al. 1999), especially during winter and at the southern extent of the species range. Juvenile bluefish have been considered estuarine dependent throughout much of the year along the MAB (Chiarella and Conover 1990; Juanes et al. 1996; Able et al. 2003; Gartland et al. 2006). Clarke (2006) contended that Florida estuaries provide all juvenile bluefish cohorts with higher prey abundances and more favorable water temperatures than nursery areas in the MAB during winter. However, relatively few individuals of the summer-spawned cohort were collected in estuaries during this sampling and no sampling occurred in the coastal ocean zone (Juanes et al. 2013). Kendall and Walford (1979) suggested that summer-spawned bluefish might never enter estuaries and select for the coastal ocean zone. Both spring- and summer-spawned cohorts of juvenile bluefish were collected in the coastal ocean of New Jersey during summer and early

autumn (Able et al. 2003). The summer-spawned cohort has also been observed in the continental shelf waters of Virginia (Gartland et al. 2006) during autumn and off the coast of North Carolina throughout this season (Morley et al. 2007).

The northern coastal ocean zone of Florida may be an under-represented habitat of juvenile bluefish especially during winter. The Florida Current along the east coast of the state during the winter produces a complex coastal temperature band which causes a steep latitudinal thermal gradient and the absence of this current on the Gulf coast results in warm winter water temperatures on the east coast of the state (Gilmore and Hastings 1983). This thermal environment in the nearshore coastal ocean along the northern Florida east coast during winter creates a sub-tropical aquatic environment for the fish fauna inhabiting what has been defined as temperate waters. The National Marine Fisheries Service (NMFS) conducts extensive spring and autumn surveys that cover much of the continental shelf from Cape Hatteras to the Gulf of Maine. However, the region from Cape Hatteras to Florida is not sampled by this survey, nor is the shallow coastal zone (<10 meters) due to the depth requirements of the survey ships. Further, the Southeast Area Monitoring and Assessment Program (SEAMAP), a State/Federal/university program that collects fishery-independent data from shallow nearshore waters of northeastern Florida does not sample during the winter. The importance of quantifying all essential habitats for economically important fishes including bluefish was underscored by NOAA's Essential Fish Habitat Program. The importance of the nearshore coastal ocean to juvenile bluefish during winter requires attention to achieve a more complete recruitment index.

CHAPTER 2

PRE-MIGRATION PATTERNS OF GROWTH, CONDITION AND RESOURCE USE BY THE SPRING- AND SUMMER-SPAWNED COHORTS OF JUVENILE BLUEFISH IN THE HUDSON RIVER ESTUARY, NEW YORK.

2.1 Introduction

For migratory fishes, attaining minimum size and energy content thresholds during the summer may be required to survive the autumn migration and subsequent overwinter period. The summer is often brief in temperate regions and can be resource limited, creating the potential for competitive interactions between individuals (Huss et al. 2008). Within a population, fish may face periods of intra-specific competition for shared resources, particularly if the resources are limited. An example being the period after age-0 juveniles migrate into a nursery habitat and compete with other members of the same cohort and/or individuals of older year-classes for food and space (Caddy 2007). For species with multiple age-classes of similar size and close proximity, interactions between age-classes may be an important source of density dependence, especially if there is a disparity in competitive ability between the cohorts (Webster 2004). It has been demonstrated that competition within size-structured populations can play an important role in population dynamics (Persson and Leonardsson 1998; Classen et al. 2000).

According to the juvenile competitive bottleneck theory (Werner and Hall 1979), young fishes with a higher foraging efficiency than individuals of a competing species may force the competitors to an earlier ontogenetic niche shift than if the competitive interaction were not present, resulting in a cost to growth and energy accumulation while

increasing the risk of predation to one or both species. Bottlenecking has been shown to occur between two competing native species (Cardona et al. 2008), among groups of native and non-native species (Walsworth et al. 2013), and within a species across age classes (Machias and Labropoulou 2002). The degree to which bottlenecking influences the vital functions of the competing species is associated with age-specific growth rate, year-class structure and recruitment timing (Scharf et al. 2006). It is reasonable to expect that the juvenile bottleneck theory could apply within a year-class of a single species if two or more cohorts are produced. However, inter-cohort competitive interactions within a single year class have rarely been investigated and may have implications for recruitment success.

One such species that produces multiple cohorts of offspring each year is bluefish (*Pomatomus saltatrix*). Bluefish reproduce along the eastern coast of the U.S. during annual spawning migrations. Although the exact temporal and spatial patterns of bluefish spawning remains uncertain, at least two cohorts (spring and summer) of offspring are produced as a result of spawning over the continental shelf (Hare and Cowen 1996). The spring-spawned cohort results from spawning in the South Atlantic Bight (SAB) from Cape Hatteras, North Carolina to Cape Canaveral, Florida (March – May), and the summer-spawned cohort originates from spawning (June – August) along the mid-Atlantic Bight (MAB) from Cape Hatteras to Cape Cod, Massachusetts (McBride and Conover 1991). Bluefish eggs and larvae develop offshore, and juveniles subsequently recruit to nearshore and estuarine waters of the MAB (Nyman and Conover 1988). Upon entry into estuaries, juvenile bluefish of both cohorts occupy more constricted habitat

than in the open ocean and are primarily piscivorous (Juanes and Conover 1994), creating

the potential for inter-cohort competition for space and food.

The Hudson River estuary (HRE) in southeast NY is composed of a seasonal assemblage

of marine, freshwater and estuarine fishes including bluefish (Beebe and Savidge 1988).

Juvenile bluefish typically recruit to the HRE in pulses; the spring-spawned cohort

arrives by late June, while the summer-spawned cohort arrives by early August and both

cohorts are abundant in the estuary throughout summer and early autumn (Scharf et al.

2006). Juvenile bluefish emigration from the HRE may be linked to water temperature

but generally occurs from early to mid-October (Juanes et al. 1993). The Hudson River

estuary represents an excellent system to evaluate the potential for a juvenile competitive

bottleneck between the spring- and summer-spawned cohorts of juvenile bluefish as it

provides for a unique opportunity to examine inter-cohort interactions prior to the fall

migration. For juvenile bluefish residing in the HRE during the summer and early

autumn, 2008 and 2009, our objectives were to; (1) use otolith microstructure analysis to

determine the cohort structure, (2) test the juvenile competitive bottleneck theory by

comparing growth and energetics, and determine the degree of food and habitat overlap

or partitioning between the spring- and summer-spawned cohorts.

2.2 Materials and methods

2.2.1 Field sampling

Fish sampling was conducted as part of the New York State Department of

Environmental Conservation (NYSDEC) juvenile fish survey from late July to early

November 2008 and 2009 at 30 fixed stations over a 65 kilometer (km) section of the

lower Hudson River estuary (Figure 2.1). Bluefish were collected with a 61 meter (m) x

3 m beach seine with 13 millimeter (mm) stretched mesh wings and a 6 mm stretched

mesh center bag. Seine hauls were set from a boat and parallel to shore. Catches were

processed on shore, with juvenile bluefish and representative forage fishes preserved

frozen for subsequent laboratory analysis. Although the water temperature was recorded

at the time and location of each seine haul, these data only represented the water

temperature on the day of sampling and didn't account for the 2 week intervals between

sampling periods. Consequently, water temperatures of the lower HRE were obtained

from the Hudson River Environmental Conditions Observing System (HRECOS), an

environmental monitoring network of high-frequency (15 minute) hydrographic

recording stations geographically distributed along the HRE and operated by a

consortium of governmental, academic, and private institutions including the NYSDEC.

We selected the George Washington Bridge hydrographic station because it was located

closest to the sampling sites in the lower HRE.

2.2.2 Water temperature analysis

To assess inter-annual and monthly differences in the water temperature of the lower

HRE, the annual water temperature was compared between years by t-test and among

months across years with one-way analysis of variance (ANOVA). January and February

2008 water temperature data were not available from HRECOS and were excluded from

the analysis. March to June water temperature data were included in the analysis to test

20

for differences in the water temperature of the lower HRE between years prior to the arrival of juvenile bluefish.

2.2.3 Cohort structure and abundance

Cohort assignments were determined by enumerating growth increments on sagittal otoliths from a sub-sample of juvenile bluefish collected throughout the summer and early autumn in 2008 and 2009. Whole otoliths were extracted and fixed to glass microscope slides with Crystalbond glass adhesive (SPI supplies), ground by hand on 600-1,200-grit silicon carbide sandpaper and polished with alumina micropolish until the daily growth increments were visible under transmitted light at magnifications of 40-100x. All microscopy and image analyses were performed with Olympus Incorporation instruments (Olympus Canada Inc., Richmond, Ontario). Hatch-dates were calculated by subtracting the number of otolith increments (age in days) from the date on which juvenile bluefish were collected in the field. Juvenile bluefish with hatch-dates prior to 21 June were assigned to the spring-spawned cohort and fish with hatch-dates after 21 June were assigned to the summer-spawned cohort. Cohort-specific catch-per-effort (CPE) of juvenile bluefish were calculated by dividing the number of bluefish from each cohort by the number of seining events during each bi-weekly sampling period.

2.2.4 Stomach content analysis

The diet contents of juvenile bluefish were examined by extracting and weighing ($\pm$ 0.01 g) the stomachs and removing all of the stomach contents. The inner walls of each stomach was scraped with a scalpel to remove any remaining contents, re-weighed (g)

and prey items were enumerated, identified to the lowest possible taxon and blotted dry.

Whole prey fishes were measured to total length (±0.10 mm TL) and weighed (±0.001 g).

For juvenile bluefish stomachs that contained partial, but identifiable remains of fish

prey, otoliths were extracted from the remains and measured (±0.001 mm) with a

dissecting stereomicroscope connected to a digital camera. To reconstruct the whole fish

total lengths (TL mm) from the partial prey found in juvenile bluefish stomachs,

representative forage fishes that were collected along with juvenile bluefish during each

bi-weekly sampling period were measured (±0.10 mm TL), and the otoliths (n = 50 per

species) were extracted and measured (±0.001 mm). The stomach contents of juvenile

bluefish were reported in frequency of occurrence (%FO; the number of stomachs in

which a prey type occurred expressed as a frequency of the total number of stomachs in

which prey were present), percent prey composition by wet weight (%W; the total weight

of a prey taxon expressed as the percentage of the total stomach content weight), and

percent prey composition by number (%N; the number of individuals of a prey taxon

expressed as a percentage of the total number of prey).

2.2.5 Feeding habits and prey phenology

For juvenile bluefish with stomachs that contained food, the gastro-somatic ratio (GSR)

was calculated as the proportion of prey weight to bluefish body weight:

$$(GSR=(FSW-ESW)/EW)$$

where FSW represented the wet weight of the stomach and its contents, ESW was the

empty stomach weight, and EW was the eviscerated bluefish weight. The GSR and

number of prey per stomach were compared between cohorts and among sampling dates

with two-way ANOVAs. If a significant interaction was detected, a Bonferroni correction ($P = 0.05/n$) was applied to account for the pair-wise type I error rate, where n was equal to the number of comparisons. The percentage of empty bluefish stomachs was compared between cohorts and among sampling periods using chi-square goodness of fit tests. To examine the predator size to prey size relationships for the spring- and summer-spawned cohorts of juvenile bluefish, partial prey lengths were converted to whole prey lengths via linear regressions between otolith length (OL) and TL (TL = α + (β*OL) of the representative forage fishes collected from the lower HRE. Converted prey sizes (TL) were compared between the juvenile bluefish cohorts and between years with 2-way ANOVA. The relationship between bluefish size (FL) and prey size was examined for the spring- and summer-spawned cohorts with least squares linear regression. Prey phenology was assessed only for bay anchovy (*Anchoa mitchilli*), the primary prey species, by dividing the number of bay anchovy collected by the number of seining events (CPE) during each bi-weekly sampling period.

2.2.6 Size and growth

Individual juvenile bluefish collected during field sampling were measured to $\pm$ 1.0 millimeters fork length (mm FL) and weighed ($\pm$ 0.1 grams wet weight). Size (FL) was compared between the cohorts during each cohabitated bi-weekly sampling period with ANOVA. The cohort-specific growth rate (mm day(d)$^{-1}$) was determined by least squares linear regressions of the mean size over time and compared between cohorts using analysis of covariance (ANCOVA), with the bi-weekly sampling date as the

covariate and cohort (spring and summer) as the explanatory variable. Fork lengths were log transformed to homogenize the variances.

2.2.7 Lipid content analysis

To determine lipid content, approximately 2-4 grams (g) of white muscle was removed from individual juvenile bluefish representing each cohort and time of residency. White muscle was selected for lipid content analysis because this tissue is an appropriate proxy for overall energy content of juvenile bluefish (Slater et al. 2007). Tissue samples were weighed (± 0.001 g), dried at 60 ºC for at least 72 hours, and re-weighed to determine dry weight and percent water weight per sample. The dry tissue was transferred to pre-weighed porous Alundum (fused alumina) thimbles for lipid extraction. An automated soxhlet extractor with di-ethyl ether was used to dissolve neutral lipids with a method similar to Shahidi (2001). After extraction, the thimbles were dried again at 60 ºC for 24 hours to ensure evaporation of any remaining solvent prior to final weighing. Weights of post-extracted dry tissue and pre-extracted dry tissue were used to determine lipid content. Lipid levels of juvenile bluefish were expressed as a proportion of the sample dry weight of white muscle and compared between the years with a t-test. Within each year, lipid content was compared between the spring and summer cohorts and among time periods with a two-way ANOVA. The Fisher's Least Significance Difference (LSD) test was used to evaluate pairwise differences in lipid content. The lipid content values of all samples were arcsine square root transformed prior to analysis due to non-normality and heterogeneous variances.

2.2.8 Competitive interactions

The level of competitive interaction between the spring- and summer-spawned cohorts was assessed using cohort-specific diet content and spatial distribution (i.e., habitat). Diet and habitat overlap between the spring- and summer-spawned cohorts was determined using Schoener's index α (Schoener 1970):

$$\alpha = 1 - 0.5\left[\sum_{i=1}^{n}|p_{ij} - p_{ik}|\right]$$

where p_{ij} = the proportion of ith resource (prey type or sampling station) used by cohort j, and p_{ik} = the proportion of the ith resource used by cohort k. The Schoener's index value ranges from 0 to 1. Values that exceeded 0.6 were considered ecologically significant overlap in resource use. Diet and habitat overlap were restricted to dates when the spring- and summer-spawned cohorts had both recruited into the Hudson River estuary.

2.3 Results

2.3.1 Water temperature

Overall, the March – October water temperature of the lower HRE was warmer (t-test = 22.27, P < 0.001) in 2008 (mean = 18.3°C) than in 2009 (mean = 16.8°C). Four (April, June, July, and October) of the eight months prior to and during juvenile bluefish residency in the HRE were warmer in 2008 than in 2009, while none of the 2009 monthly mean water temperatures were significantly higher than in the preceding year (Figure 2.2).

2.3.2 Cohort structure and abundance

A total of 788 juvenile bluefish were collected from the Hudson River estuary during the summer and early autumn in 2008 (n = 310) and 2009 (n = 478) combined. Hatch-date to length relationships of sub-samples of juvenile bluefish representing each bi-weekly sampling period in 2008 (n = 47) and 2009 (n = 40) were used to construct total cohort-specific hatch-date distributions for the remaining bluefish collected in each year. In both years, back-calculated hatch-date distributions were bimodal, indicating the occurrence of spring- and summer-spawned cohorts of juvenile bluefish. Peak hatch-dates for the spring- and summer-spawned cohorts occurred in mid-April and late June respectively in 2008 and approximately one to three weeks later for each cohort in 2009 (Figure 2.3).

In 2008, the combined CPE of both juvenile bluefish cohorts was more than 3 times higher in July (CPE_{July} = 3.8 fish seine^{-1}) than August, September and October and the overall cohort-specific catch rates of spring-spawned bluefish (CPE_{total} = 1.72 fish seine^{-1}) were higher than the summer-spawned cohort (CPE_{total} = 0.81 fish seine^{-1}). The juvenile bluefish catches were comprised of exclusively spring-spawned fish during the first sampling event in mid-July 2008. Catch-per-effort of spring-spawned fish declined throughout the remainder of the summer in 2008 and this cohort emigrated from the HRE by the end of August. The summer-spawned cohort first appeared in the HRE in late July 2008 and constituted approximately 50% of the bluefish catch by mid-August. Summer-spawned fish CPE peaked at the end of August 2008, but were collected from the lower HRE until early October (Figure 2.4).

In 2009, field sampling began two weeks later than in 2008, but differences in juvenile bluefish cohort dynamics were evident between years. The greatest catch rates of juvenile bluefish occurred more than 1 month later in 2009 than in 2008, and the overall cohort structure was dominated by summer-spawned bluefish in 2009 (CPE_{total} = 2.62 fish seine^{-1}, Figure 2.4). In early August 2009, the CPE of juvenile bluefish was the lowest of the sampling period and only spring-spawned fish were collected, while peak CPE of the spring-spawned cohort occurred approximately one month later in 2009 than in the previous year (Figure 2.4). Summer-spawned fish arrived to the HRE in mid-August 2009 and constituted approximately 40% of the juvenile bluefish catch during this sampling period. Summer-spawned bluefish CPE peaked one week later and was four times greater in 2009 than 2008. Bluefish CPE was dominated by summer-spawned fish until the end of the study period and catch rates of both cohorts combined were nine times greater in October 2009 ($CPE_{Oct.}$ = 0.71 fish seine^{-1}) than October 2008 ($CPE_{Oct.}$ = 0.08 fish seine^{-1}) and bluefish were still being collected through the middle of October 2009 (Figure 2.4).

2.3.3 Feeding habits and prey phenology

Bay anchovy was the most abundant prey species of juvenile bluefish in 2008 and 2009, contributing to over 70% of the stomach contents across all diet indices (Table 2.1). The second most abundant prey to the diet composition of juvenile bluefish was striped bass, occurring in only 5.5% of bluefish stomachs. No other prey fishes contributed more than 5% to the diets in any of the diet indices.

The GSR of the summer-spawned cohort (mean = 2.05 %) was higher (P < 0.05) than the spring-spawned cohort (mean = 1.66 %) in 2008 and was similar (P = 0.54) between the cohorts in 2009. During the summer of 2008, the GSR decreased in spring-spawned juvenile bluefish and increased in the summer-spawned cohort, while the GSR decreased in both cohorts over time in 2009 (Table 2.2). Juvenile bluefish of both cohorts typically had between 1.0 and 1.5 prey in their stomachs and the number of prey per stomach were similar between the 2 cohorts in both years (P > 0.10). The percentage of empty stomachs was higher in the summer-spawned cohort (40.0%) than the spring-spawned cohort (26.8%) in 2008, while more spring-spawned fish (52.0%) had empty stomachs than summer-spawned fish (35.3%) in the following year. The temporal trend in the percentage of empty stomachs was opposite to the GSR for each cohort in 2008, but was consistent in both cohorts over time in 2009 (Table 2.2).

Bay anchovy was the single important (> 70.0 %, no other prey > 6%) prey fish found in the stomachs of juvenile bluefish. Consequently, the linear regression between OL and TL used for reconstructing whole prey size was calculated only for this species ((TL = 32.1 + (7.9*OL), n = 57, R^2 = 0.97, P < 0.001)). Reconstructed bay anchovy lengths were similar to the TL of whole prey found in the stomachs of juvenile bluefish in both years (P > 0.10). In 2008 and 2009 combined, spring-spawned juvenile bluefish consumed bay anchovy (mean TL = 66.3 mm, n = 197) approximately two times larger (t-test = 21.2, P < 0.001) than the bay anchovy (mean TL = 32.9 mm, n = 110) consumed by the summer-spawned cohort. The bi-modal distribution in the prey sizes consumed by juvenile bluefish was consistent across both years of the study (Figure 2.5). A

positive predator to prey size relationship ($R^2 = 0.22$, $P < 0.01$) was observed between the

summer-spawned cohort and bay anchovy, while no relationship in size was evident ($P =$

0.33) between the spring-spawned bluefish predators and the bay anchovy prey (Figure

2.6). The predator to prey size relationships were consistent for the two cohorts across

both years of the study.

Similar to the inter-annual difference in the abundance of juvenile bluefish in the lower

HRE, the overall CPE of bay anchovy was sixteen times greater in 2009 than in 2008.

Two peaks in the catches of bay anchovy were evident in both years, occurring

approximately two weeks earlier in 2009 than in the previous year (Figure 2.7). In 2008,

the CPE of bay anchovy was low (< 1.0 fish seine^{-1}) until the end of August peak, and

similarly low again until after both cohorts had emigrated from the lower HRE. In 2009,

the CPE of bay anchovy was greater than the previous year during all but one of the

sampling periods while spring- and summer-spawned juvenile bluefish inhabited the

lower HRE (Figure 2.7).

2.3.4 Size and growth

In 2008, the sizes of juvenile bluefish collected from the HRE ranged from 43 – 192 mm

FL (mean FL = 125 mm). Spring-spawned juvenile bluefish were larger than summer-

spawned fish during all bi-weekly sampling periods ($F_{7,198} = 33.8$, $P < 0.001$, Figure 8) in

2008, but growth was greater in the summer-spawned cohort (1.59 mm d^{-1}) than the

spring-spawned cohort (1.02 mm d^{-1}) during estuarine residency. In 2009, bluefish sizes

ranged from 46 to 210 mm FL (mean FL = 104 mm). Similar to 2008, spring-spawned

juvenile bluefish were larger than the summer-spawned cohort throughout the entire 2009 sample year ($F_{10,476} = 155.9$, $P < 0.001$), but the growth rate of spring-spawned fish (1.25 mm d^{-1}) was greater than summer-spawned fish (0.89 mm d^{-1}).

Although sampling did not occur on the same date during each year of the study, within-cohort size differences were evident between years, but only within the summer-spawned cohort (Figure 2.8). Summer-spawned juvenile bluefish arrived to the HRE almost three weeks earlier in 2008 than in 2009 and were predictably smaller (mean FL = 46 mm) upon estuarine arrival in this year than in 2009 (mean FL = 64 mm). However, summer-spawned fish grew quickly during the first two weeks of estuarine residency in 2008 and were larger ($P < 0.001$) on 13 August 2008 than on 18 August 2009 when the cohort arrived into the HRE (Figure 2.8). Summer-spawned fish were also larger ($P < 0.001$) during the subsequent sampling period in 2008 (27 August, mean FL = 106 mm) than the closest corresponding date in 2009 (02 September, mean FL = 84 mm). Summer-spawned fish were approximately the same size (mean FL = 117 mm) between years upon emigration from the HRE, but emigration occurred 1 month earlier in 2008 than in 2009. Spring-spawned juvenile bluefish were similar in size between years ($P > 0.10$) during all of the closest corresponding bi-weekly sampling periods, but the spring-spawned cohort was 34 mm larger in early October 2009 than late August 2008 when they began their autumn migration out of the HRE.

2.3.5 Lipid content

Overall, the lipid content of juvenile bluefish was higher (t-test = 4.5, P < 0.001) in 2008

(mean ± s.e. = 5.42 ± 0.19%, n = 50) than 2009 (mean ± s.e. = 3.84 ± 0.24%, n = 66), and

the two-way ANOVAs showed that the lipid content of the juvenile bluefish was

influenced by both cohort and sampling date during both years of the study (Table 2.3).

The lipid content of the summer-spawned cohort (2008, mean ± s.e. = 5.57 ± 0.29%, n =

24; 2009, mean ± s.e. = 4.91 ± 0.35%, n = 32) was higher (P < 0.05) than the spring-

spawned cohort (2008, mean ± s.e. = 4.55 ± 0.20%, n = 26; 2009, mean ± s.e. = 3.30 ±

0.29%; n = 34) in both years of the study. The significant interaction between cohort and

sampling date in 2008 (Table 2.3) was driven by the higher lipid content during the

sampling periods when only the spring-spawned (15 July) or summer-spawned (11

September) cohort inhabited the lower HRE (Figure 2.9).

In 2008, lipid levels were similar (P = 0.86) between the cohorts upon arrival of summer-

spawned fish to the HRE in 2008, but increased in the summer-spawned cohort and

decreased in spring-spawned fish throughout the summer (Figure 2.9). A similar trend in

lipid content was observed during the summer of 2009 as during the 2008 study period,

wherein the percentage of lipid in dried bluefish muscle tissue was similar between the

two cohorts during the first sampling period when both cohorts inhabited the HRE

together and higher in the summer-spawned cohort throughout September (P < 0.01).

However, the lipid content of both cohorts declined in early autumn (01 October 2009),

particularly in the summer-spawned cohort, decreasing to the lowest lipid level of the

year by the last sampling date in mid-October (Figure 2.9).

2.3.6 Competitive interactions

In 2008, the spring-and summer-spawned cohorts of juvenile bluefish cohabited the lower HRE from 29 July to 27 August, but the evaluation of diet and habitat overlap was limited to the two sampling dates in August due to low catch rates of the summer-spawned cohort on 29 July (n = 7). Diet overlap was high between the two cohorts during August 2008, while spatial examination of the cohort-specific distribution showed low habitat overlap between the two cohorts (Table 2.4). In August 2008, cohort-specific catches of spring-spawned versus summer-spawned bluefish occurred at 13 stations and 15 stations respectively, while overlap between the cohorts occurred at only 3 stations.

In 2009, both cohorts of juvenile bluefish did not fully recruit to the lower HRE until mid-August, but a similar trend in the diet overlap was observed as in 2008 (Table 2.4)**.** Overlap in feeding was high (Shoener's $\alpha > 0.70$) between spring- and summer-spawned juvenile bluefish throughout the late summer of 2009. Diet overlap decreased from August to early October 2009 as striped bass (*Morone saxatalis*), Atlantic silversides (*Menidia menidia*), and banded killifish (*Fundulus diaphinus*) appeared in the diets of spring-spawned bluefish, while the summer-spawned cohort continued to feed almost exclusively on bay anchovy. Similar to 2008, spatial overlap between the spring- and summer-spawned cohorts of juvenile bluefish was consistently low in 2009 (Shoener's α < 0.40. Table 2.4).

2.4 Discussion

2.4.1 Cohort structure and abundance

For fishes that reproduce within a discrete time period and produce a single cohort of offspring, juvenile recruitment potential can be determined by stochastic environmental events, thus increasing inter-annual recruitment variability (Munch and Conover 2000). However, producing multiple cohorts of young across numerous spawning events dampens recruitment variability by spreading the mortality risk out over time and space (Secor 2007), and a single catastrophic environmental event is less likely to overwhelm an entire year class. In the present study, peaks in the hatch-date distributions of mid-April and late June/early July indicated that the juvenile bluefish inhabiting the lower HRE were produced from two primary spawning events in the spring and summer respectively. The timing of these two spawning periods was consistent with previous investigations of bluefish reproduction in other Atlantic coast estuaries (Taylor et al. 2007; Callihan et al. 2008). Multiple spawning events resulting in two or more cohorts of offspring may contribute to higher juvenile survival rates for bluefish.

The cohort structure of juvenile bluefish that recruited to the lower HRE was dominated by spring-spawned fish in 2008 and summer-spawned fish in 2009. The contribution of the two cohorts to the western Atlantic adult bluefish population has varied over a multi-decadal scale. During the 1950s, the relative abundance of the spring-and summer-spawned cohorts of juvenile bluefish was nearly equal (Lassiter 1962). From the mid 1970s through the 1980s spring-spawned bluefish dominated the cohort structure in the MAB (Munch and Conover 2000). An apparent shift in bluefish recruitment favored the

summer-spawned cohort throughout much of the last two decades, but summer-spawned fish did not contribute proportionally to the adult population and low recruitment of this cohort has been implicated in the recent decline of the western Atlantic bluefish stock (Conover et al. 2003). Consequently, incorporating the contribution of spring- and summer-spawned bluefish to juvenile abundance indices on an annual basis could contribute to better recruitment forecasts and ultimately improvements in bluefish management.

The peak hatch dates of the spring- and summer-spawned cohorts of juvenile bluefish occurred approximately one and three weeks later respectively in 2009 than in 2008, corresponding to similar delays in the arrival of the summer-spawned cohort to the lower HRE and the later dates of maximum CPE for both cohorts. In the U.S., bluefish are thought to spawn along the inner-continental shelf of the SAB in the spring and the MAB in the summer as ocean temperatures surpass 18°C (Norcross et al. 1974). Larvae and juveniles are found in water temperatures between 18 – 26°C (Kendall and Walford 1979) and do not tolerate water temperatures less than 13°C (Hare and Cowen 1996). The water temperatures of the lower HRE during the late summer and early autumn corroborated the temperature preferences of juvenile bluefish and were higher than 15°C through October in both years, but the water temperature analysis for the period when the two cohorts occupied the estuary did not provide conclusive evidence for the differential cohort-specific recruitment timing between the two years of the study. However, the average water temperature of the lower HRE in the four months prior to the arrival of juvenile bluefish was warmer in 2008 than 2009, particularly during the two months that

34

corresponded to the peak hatch dates of the two cohorts, indicating a link between spring and early summer water temperatures and adult bluefish spawning, and ultimately juvenile bluefish entry timing to the lower HRE. Hence, monitoring the water temperature in regions where juvenile bluefish typically recruit to after hatching, but in advance of their arrival could be used as a tool to better understand bluefish phenology in other regions.

Juvenile bluefish typically emigrate from MAB estuaries en route to southern or offshore overwintering habitats as water temperatures fall below 15°C (Juanes et al. 1996) and are absent from MAB estuaries by mid-October (Able et al. 2003). In the present study, the water temperature of the lower HRE began to decline during September of both years, but remained above 15°C through October. We found that the spring-spawned cohort emigrated from the lower HRE by the beginning of September in 2008, while individuals of both cohorts were still being collected more than a month later into mid-October in 2009. Moreover, the average summer and early autumn water temperatures remained more than 1.0°C higher in 2008 than 2009. Accordingly, we expected longer residence times in the lower HRE of both cohorts during 2008 than the cooler 2009, but the opposite was observed. One possible explanation for the unexpected discrepancy in emigration timing of the two cohorts from the lower HRE between years may be the temporal dynamics in the abundance bay anchovy, the most important prey to juvenile bluefish in both years. Taylor et al. (2007) showed a positive relationship between prey (bay anchovy abundance and Atlantic silversides) and juvenile bluefish CPE along the New Jersey coast, but didn't distinguish this relationship for each bluefish cohort. In the

present study, bay anchovy CPE was low during all but two of the sampling events in 2008; the first peak occurring during the latest date that spring-spawned bluefish inhabited the lower HRE and the second happening after both cohorts had already emigrated from the estuary. Conversely, bay anchovy were relatively more abundant in the lower HRE through mid-October of the following year and the initial peak in CPE occurred one to two weeks prior to the greatest abundance of the spring- and summer-spawned cohorts of juvenile bluefish respectively, corresponding to the longer residence time of both cohorts. Juanes et al. (1994a) found that the arrival and peak CPE of Atlantic silversides in the HRE occurred just prior to the peak abundance of juvenile bluefish over a four year period suggesting that the timing of bluefish ingress to juvenile nursery habitats may be driven by the phenology of their prey. The results of the present study indicate that the timing and duration of prey production in the HRE likely influences the timing of juvenile bluefish egress from the estuary as well, especially when water temperatures remain in the preferred range for this species.

2.4.2 Feeding habits

The feeding behavior of juvenile bluefish has been described in MAB waters (Buckel et al. 1999b; Able et al. 2003; Gartland et al. 2006), including the Hudson River estuary (Juanes et al. 1993; Juanes et al. 1994). Therefore, our objective was to extend upon the diet description of bluefish in the HRE to examine the inter-cohort interaction in feeding ecology. In 2008 and 2009, the stomach contents of spring- and summer-spawned juvenile bluefish inhabiting the lower HRE were dominated by bay anchovy. The selection for bay anchovy by juvenile bluefish has been well documented (Buckel and

Conover 1997; Woodland and Secor 2011), but our approach identified temporal trends in the feeding intensity of the two cohorts. The within-year decline and between-year difference in the GSR of spring-spawned fish reflected the inter-annual variability in bay anchovy abundance, while the opposite trend in GSR of summer-spawned fish, particularly in 2008 indicated an interaction between the cohorts that was not revealed in bay anchovy abundance alone. Juanes et al. (1993) used a size-based approach to summarize the cohort-specific diet content of juvenile bluefish and showed an ontogenetic shift in prey species, from bay anchovy in small bluefish to Moronids and Atlantic tomcod (*Microgadus tomcod*) in medium to large sized bluefish respectively. Although striped bass were found in 5.5% of bluefish stomachs, we did not observe such a shift in prey type with increasing bluefish size.

The positive relationship between predator size and prey size has been well established for fishes (Juanes et al. 2002), including juvenile bluefish (Juanes et al. 1994; Buckel et al. 1999a). Scharf et al. (2002) showed that juvenile bluefish capture success on bay anchovy declined with increasing bay anchovy size but remained relatively high up to anchovy sizes 50% of bluefish sizes. Interestingly, we found that summer-spawned bluefish consumed larger bay anchovy with increasing size, but spring-spawned fish preyed upon a relatively narrow range of bay anchovy sizes with a prey to predator size ratio of 50%. Although Scharf et al. (2002) did not separate juvenile bluefish into spring- and summer-spawned cohorts, fish sampling was conducted in June, and hence all of the bluefish were likely spring-spawned individuals. The non-significant relationship in size

between spring-spawned bluefish and bay anchovy observed here represents a unique feeding strategy for this cohort.

The strong relationship between bay anchovy otolith length and total length over a range of bay anchovy voucher sizes allowed us to reconstruct whole prey sizes from the partial remains found in juvenile bluefish stomachs.   The multi-modal size distribution of prey consumed by spring- and summer-spawned juvenile bluefish indicated that the two cohorts selectively fed on different age groups of bay anchovy. Larval and juvenile (age-0) bay anchovy inhabiting the HRE are typically less than 55 mm TL (Hartman et al. 2004).   Basista and Hartman (2005) determined that the sub-adult and adult age composition of bay anchovy in the HRE consists of age-1 fish less than 65 mm TL, age-2 fish ranging from 61 to 94 mm TL, age-3 fish greater than 79 mm, and age-4 fish greater than 93 mm TL, with age-2 and older fish constituting the spawning population. Our results showed that summer-spawned juvenile bluefish largely preyed upon juvenile (age-0) and sub-adult (age-1) bay anchovy in 2008, and smaller larval and juvenile bay anchovy in the following year, while the spring-spawned cohort consumed mostly adult (age-2,-3) bay anchovy in both years. These findings have important implications for the recruitment dynamics of juvenile bluefish and population dynamics of bay anchovy, depending on annual trends in the cohort structure of juvenile bluefish, and the timing and magnitude of bay anchovy production.

2.4.3 Growth and energetics

We found that the summer-spawned cohort grew faster than spring-spawned fish in 2008, while the opposite growth response was evident between the two cohorts in the following year. Summer-spawned bluefish may be expected to grow faster than spring-spawned individuals in order to compensate for the size advantage incurred by the earlier hatching of spring-spawned fish (Juanes and Conover 1995). Faster growth rates of the summer-spawned cohort than the spring-spawned cohort have been reported in other areas of the MAB, but spring-spawned fish were still larger than summer-spawned fish at the onset of the autumn migration (McBride and Conover 1991; Taylor et al. 2007). Similarly, we found that spring-spawned juvenile bluefish maintained the size advantage over the summer-spawned cohort by the time of emigration from the lower HRE in both years irrespective of the cohort-specific growth rate. Conover et al. (2003) suggested that the disproportionately low contribution of the summer-spawned cohort to the adult population may be the result of high size-selective overwinter mortality of small summer-spawned fish. Fish mortality during periods of cold stress has been related to size, with smaller individuals suffering higher mortality rates than their larger conspecifics (Sogard 1997; Hurst 2007). If summer-spawned bluefish are failing to recruit to the adult population, it may be attributed to the inability of this cohort to compensate in growth to spring-spawned fish by the time of the autumn migration.

The variable growth rates of spring- and summer-spawned juvenile bluefish between years may be associated with the densities of the two cohorts within each year. Scharf et al. (2006) experimentally demonstrated that the growth rates of early arriving summer-

spawned fish would be greater than late arriving fish in years when the initial density of

spring-spawned fish was low. We found that summer-spawned fish arrived earlier in

2008 than 2009 to relatively high spring-spawned cohort densities, but grew faster in this

year than in 2009 when arriving later to relatively low spring-spawned bluefish densities.

Moreover, the slowest growth rate of the summer-spawned cohort occurred in 2009 at the

highest density of summer-spawned fish, indicating that summer-spawned bluefish

growth rates may have been less dependant on the density of spring-spawned fish than on

the density of individuals from their own cohort.

To our knowledge, this study represents the first examination of the lipid content in

juvenile bluefish during the summer prior to the autumn migration. Migratory fishes

inhabiting temperate waters typically accumulate energy stores in the summer, especially

during periods of maximum feeding opportunities and optimal water temperature

(Rikardsen et al. 2006; Chicharo et al. 2012). In the present study, the water temperature

of the lower HRE increased through August and was in the optimal range of juvenile

bluefish (Hartman and Brandt 1995) during the entire summer in both years, thus we

expected the lipid levels in both cohorts of juvenile bluefish to increase during this time

in preparation for the autumn migration. We found this to be the case for the summer-

spawned cohort in both years but not for spring-spawned fish in either year. The lipid

content in the spring-spawned cohort was highest during the sampling period just prior to

the arrival of summer-spawned fish, but precipitously declined over the next month and

remained relatively low until emigrating from the estuary, while summer-spawned fish

arrived to the lower HRE with the lowest lipid levels of the summer and subsequently

accumulated energy reserves for the remainder of the season. Spring-spawned juvenile

bluefish arrive to the lower HRE from mid to late June (Hare and Cowen 1996), so we

likely missed the first collection of this cohort by at least one bi-weekly sampling period.

Consequently, it was not possible to determine the energetics of the spring-spawned

cohort upon first appearance in the lower HRE similar to what we were able to discern

for summer-spawned fish. Nevertheless, the inverse trends in lipid content between the

two cohorts over both summers of this study warrants further consideration.

Within a species, the lipid levels of juvenile fish can be influenced by ambient

temperature (Merayo 1996; Luzia et al. 2003), prey quality and quantity (Kiessling et al.

1989; Daly et al. 2010), somatic size (Copeman et al. 2008; Heermann et al. 2009) and/or

physiological factors (Griffiths and Kirkwood 1995). Although the spatial overlap

between spring- and summer-spawned juvenile bluefish was low, the two cohorts likely

experienced equivalent water temperatures while co-habiting the lower HRE, therefore

temperature could be effectively ruled out as a cause of the differential energetics

between the two cohorts. In both years of the study, the summer-spawned cohort did not

recruit to the HRE until at least two weeks after spring-spawned fish, thus it is possible

that an earlier dietary shift by the spring-spawned cohort from low energy invertebrate

prey to a more lipid rich fish diet (Buckel et al. 1998) resulted in higher initial energy

content of spring-spawned fish, while the summer cohort arrived to the lower HRE with a

mid-summer lipid deficit. A novel discovery of the present study was the similarity in

prey type between spring-spawned and summer-spawned fish while the two cohorts co-

occurred in the lower HRE, in that both cohorts consumed almost exclusively bay

anchovy. Resultantly, prey quality was also unlikely responsible for the lipid content dynamics of the two cohorts during the summer allowing us to investigate the quantity of food as the potential explanatory factor. In 2008, the GSR and percentage of empty stomachs in the spring-spawned cohort decreased and increased respectively during the summer, while the complete opposite trends in these diet metrics were observed in the summer-spawned cohort. The relationships between lipid content and feeding intensity were not as direct during the summer of 2009 as in the previous year, but the general trends were maintained. With respect to size, the higher lipid content in smaller summer-spawned fish over most of the summer conflicted with previous observations of the relationship between somatic size and energy resources, wherein larger fish typically contain greater energy stores than smaller fish within the same year-class (Schultz and Conover 1997; Hurst and Conover 2003) including bluefish (Juanes et al. 2013). The concept of smaller fish within a year-class containing lower lipid content is thought to be due a higher mass-specific metabolic rate and subsequent faster depletion of lipids than in the larger individuals (Post and Lee 1996), particularly during winter. However, Morley et al. (2007) collected larger juvenile bluefish with greater energy reserves from North Carolina waters in autumn, but the larger fish lost this energetic advantage during the winter due to faster energy depletion with increasing somatic size. Moreover, Slater et al. (2007) experimentally showed that the larger spring-spawned cohort began the winter with greater lipid content than summer-spawned fish, but the two cohorts had similar energy reserves by early spring. Unfortunately, there isn't an evaluation of the lipid content in juvenile bluefish during the summer to compare our results, but we found the greatest difference in lipid content between the cohorts at the end of the summer, in

42

which the smaller summer-spawned cohort contained higher energy stores than larger spring-spawned fish. This suggests that lipid content may not be as size-dependent as previously assumed and perhaps a cohort-specific physiological tradeoff or constraint between growth and energy utilization exists in juvenile bluefish.

Smaller juvenile fish within a year-class reduce predation risk by allocating resource intake to growth rather than energy storage, while larger individuals dedicate resources to storing energy over growth to avoid starvation during the winter (Sogard 1997; Post and Parkinson 2001). Under this paradigm, we expected the smaller summer-spawned cohort to dedicate as much resource intake as possible to growth over lipid accumulation during the summer. Although summer-spawned bluefish grew faster than spring-spawned fish in 2008, they were still considerably smaller than spring-spawned fish by the end of the summer, yet stored more energy than their larger conspecifics during the summer in both years. Juvenile bluefish are already piscivorous when they arrive to the HRE (Scharf et al. 2004) and likely do not experience high rates of predation during the summer (Sagarese et al. 2011). With the risk of predation low, juvenile bluefish of both cohorts inhabiting the HRE during the summer may dedicate more food resources to energy storage than growth in preparation for the autumn migration, and the contrasting trends in energy utilization between the two cohorts during the summer of 2008 and 2009 were primarily attributed to temporal differences in the feeding intensity exhibited by each cohort.

Temperate fishes have been shown to deplete energy resources during the autumn and winter due to reductions in feeding and temperature (Hurst et al. 2000; Brodersen et al. 2011). In the present study, the spring- and summer-spawned cohorts of juvenile bluefish emigrated from the lower HRE by early October 2008 when water temperatures were still above 18°C, precluding the evaluation of pre-migration autumn energetics. However, concomitant with water temperatures declining below 18°C in the lower HRE, the lipid levels of both cohorts declined through October 2009 until emigrating from the estuary. Morley et al. (2007) showed that the lipid content of overwintering juvenile bluefish in North Carolina waters increased from October to November before declining along with CPE throughout the winter. Further, both lipid content and catch rates of juvenile bluefish increased during the winter in northern Florida coastal estuaries (Juanes et al. 2013). Interestingly, the water temperatures during October and November in North Carolina waters (Morley et al. 2007), and over the winter along the northern Florida coast (Juanes et al. 2013) were similar to the lower HRE during the summer and within the preferred range (18 – 26°C) of juvenile bluefish. This suggests that a rapid decline in lipid content during early autumn in northern MAB estuaries like the lower HRE may trigger juvenile bluefish to begin a southerly migration, and subsequent declines in condition during late autumn/early winter in the southern MAB promotes movement farther south to overwinter in SAB waters, and is driven by both abiotic and biological factors.

2.4.4 Competitive interactions and the juvenile bottleneck

According to the juvenile competitive bottleneck hypothesis, a species with higher

foraging efficiency may force another species to an earlier ontogenetic niche shift during

the first summer of life, resulting in a cost to growth, and energy accumulation while

increasing the risk of predation (Werner and Hall 1979). We observed a high level of

habitat partitioning between the spring- and summer-spawned cohorts during the summer

and early autumn in 2008 and 2009, such that members of either cohort were collected

independent of the other at fifty eight stations while the cohorts occurred together in low

relative abundance at thirty stations during simultaneous residency of the lower HRE.

Although we can't rule out the possibility of the larger spring-spawned cohort forcing the

younger/smaller con-specifics to alternative habitats in the HRE, neither cohort of

juvenile bluefish appeared to be resource limited during both years of this study and a

cost to growth and condition was not apparent in summer-spawned fish. Juvenile

bluefish are already upper level predators upon arrival to the HRE, thus cannibalism

would likely be the primary source of predation. Although cannibalism can influence the

size structure of fish populations (Claessen et al. 2000; Persson et al. 2004), it was not

evident in 2008 and only observed during the first sampling period in 2009.

For fishes like bluefish that produce two or more cohorts within a year class, the feeding

preferences on a single prey species may be similar among the cohorts leading to the

appearance of high intra-specific competition. However, age-class selective feeding such

as observed here can result in the actuality of low intra-specific competition. Our results

indicate that in a large estuary like the HRE, the spring- and summer-spawned cohorts

45

avoided intra-specific competition by separating their niches in the spatial dimension and fed on different age-classes of bay anchovy. This niche separation widened or eliminated the juvenile competitive bottleneck, such that summer-spawned fish did not appear to suffer any negative consequences to occupying different habitats than their older conspecifics during the first summer of life.

Table 2.1. Diet composition of juvenile bluefish. Fish were collected from the lower Hudson River estuary in 2008 and 2009 (%N; the number of individuals of a prey taxon expressed as a percentage of the total number of prey, %W; the total weight of a prey taxon expressed as the percentage of the total bluefish stomach content weight, %FOO; the number of bluefish stomachs in which a prey type occurred expressed as a frequency of the total number of bluefish stomachs in which prey were present).

Prey item	%N	%W	%FOO
Vertebrata			
Engraulidae			
Anchoa mitchilli	75.35	71.36	72.25
Anchoa hepsetus	0.398	2.05	0.524
Clupeidae			
Alosa sapidissima	0.398	0.102	0.524
Alosa pseudoharengus	0.596	0.78	0.786
Alosa aestivalis	0.596	0.306	0.785
Brevortia tyrannus	0.6	0.52	0.79
unidentified clupeidae	1.39	3.28	1.83
Moronidae			
Morone saxatilis	4.18	6.5	5.5
Morone americana	0.199	0.3	0.262
Pomatomidae			
Pomatomus saltatrix	1.19	2.37	1.57
Gadidae			
Microgadus tomcod	0.994	2.09	1.31
Atherinidae			
Menidia menidia	3.78	4.77	4.415
Fundulidae			
Fundulas diaphinus	2.54	4.1	3.43
Unidentified fish	4.2	1.339	29.445
Invertebrata			
Amphipoda	3.0	0.125	5.24
Copepoda	0.389	0.004	0.524
Decapoda	0.2	0.004	0.26

47

Table 2.2. Feeding intensity of juvenile bluefish. Fish were collected from the lower Hudson River estuary in 2008 and 2009. Spring and summer represent spring-spawned and summer-spawned cohorts. Differences in gastro-somatic ratio, number (No.) of prey per stomach and percent (%) empty stomachs among dates (rows) and between cohorts (columns) are represented by different alphabetic and numeric superscripts respectively.

	Gastro-somatic ratio		No. prey per stomach		% empty stomachs	
	Spring	Summer	Spring	Summer	Spring	Summer
2008						
15 Jul.	2.49^a	----	1.22^a	----	21.2^a	----
29 Jul.	1.72^{b1}	1.74^{a1}	1.20^{a1}	1.00^{a1}	23.3^{a1}	100.0^{a2}
13 Aug.	1.23^{c1}	1.99^{a2}	1.17^{a1}	1.46^{b2}	26.5^{a1}	58.2^{b2}
27 Aug.	1.20^{c1}	2.17^{b2}	1.16^{a1}	1.50^{b2}	56.5^{b1}	58.4^{b1}
11 Sep.	----	2.32^b	----	1.48^b	----	22.3^c
Year avg.	1.66^1	2.05^2	1.20^1	1.36^1	26.8^1	40.0^2
2009						
04 Aug.	3.57^a	----	1.25^{ab}	----	52.6^{ab}	----
18 Aug.	2.06^{b1}	4.91^{a2}	1.20^{ab1}	1.20^{a1}	42.4^{a1}	31.8^{a1}
02 Sep.	1.10^{c1}	1.88^{b2}	1.00^{a1}	1.25^{a1}	60.0^{b1}	37.8^{a2}
15 Sept.	0.75^{c1}	1.06^{c1}	1.12^{a1}	1.24^{a1}	63.6^{b1}	31.0^{a2}
1 Oct.	1.41^{b1}	2.15^{b1}	1.50^{b1}	1.20^{a2}	60.0^{b1}	33.3^{a2}
15 Oct.	----	2.65^b	----	1.47^a	----	32.0^a
Year avg.	2.00^1	2.10^1	1.17^1	1.30^1	52.0^1	35.3^2

Table 2.3. Summary of the two-way ANOVA on the effects of cohort and sampling date on the lipid content (% dried white muscle). Juvenile bluefish were collected from the lower Hudson River estuary during the summer and early autumn 2008 and 2009.

Year	Factor	d.f.	SS	MS	F-value	P
2008	Cohort	1	8.49	8.49	6.00	0.017*
	Date	4	31.85	7.96	5.64	0.000**
	Cohort x Date	4	10.48	3.49	2.65	0.050*
	Error	40	55.03	1.31		
2009	Cohort	1	30.94	30.94	11.81	0.001**
	Date	5	62.38	12.48	3.84	0.004**
	Cohort x Date	5	16.67	4.17	1.59	0.189
	Error	54	146.75	2.62		

d.f., degrees of freedom; SS, sum of squares; MS, mean squares. $*P \leq 0.05$; $**P \leq 0.01$

Table 2.4. Schoener's overlap index (α) for diet (species) and habitat (station) between the spring-and summer-spawned cohorts. Juvenile bluefish were collected from the lower Hudson River estuary in 2008 and 2009.

Sampling date	Diet type	Habitat
13 Aug. 2008	0.87	0.30
27 Aug. 2008	0.93	0.24
18 Aug. 2009	0.85	0.24
02 Sep. 2009	0.79	0.38
15 Sep. 2009	0.70	0.30
01 Oct. 2009	0.57	0.40
Average	0.79	0.27
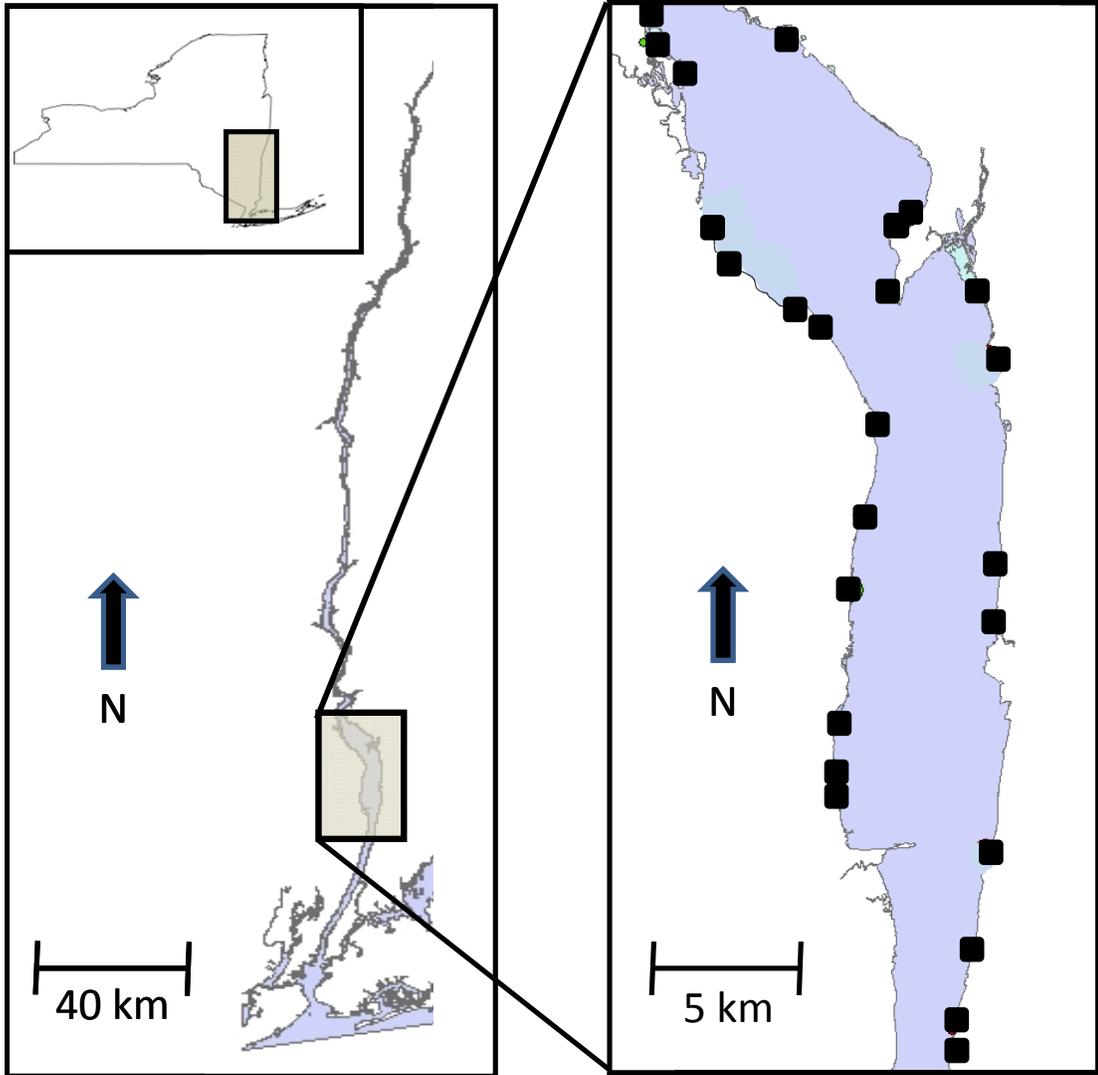
Figure 2.1. Map of the study area in the lower Hudson River Estuary, New York. The fixed stations sampled by the New York State Department of Environmental Conservation are represented by black squares.
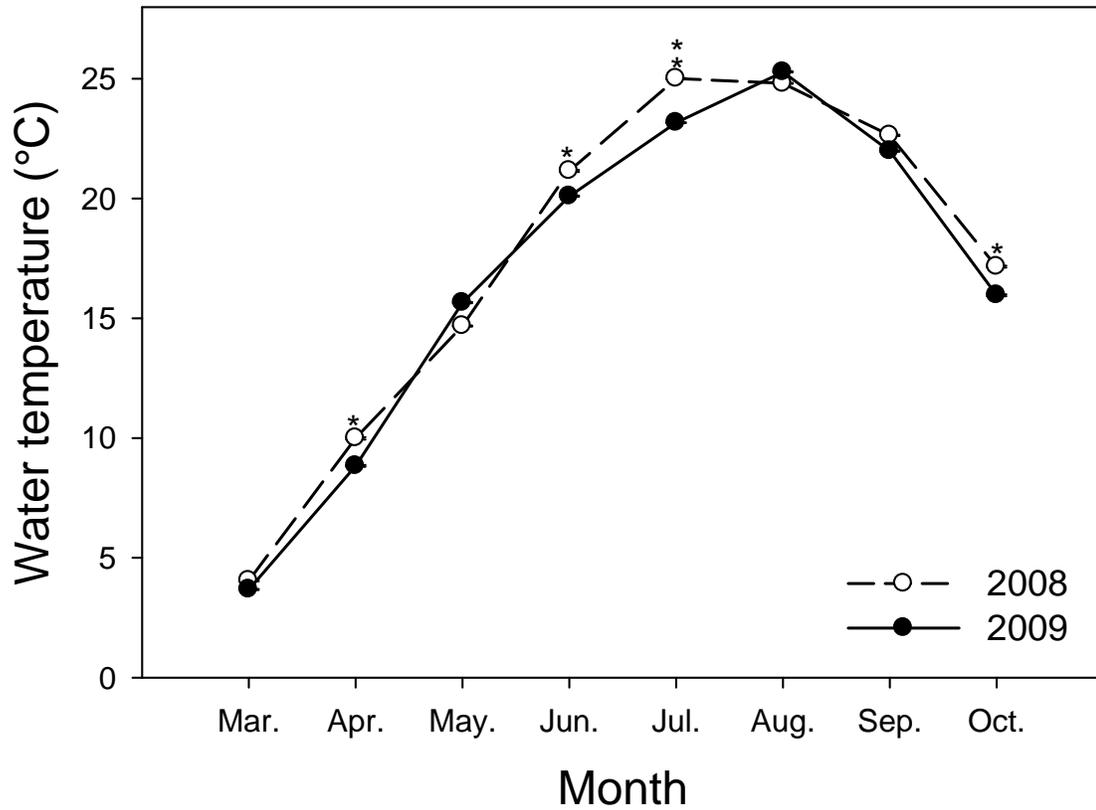
Figure 2.2. Water temperature profiles of the lower HRE from March through October. The water temperatures were recorded by the Hudson River Environmental Conditions Observing System (HRECOS) George Washington Bridge hydrographic station. Differences in mean monthly water temperatures are represented by a single asterisk (P < 0.01) or double asterisks (P < 0.001).
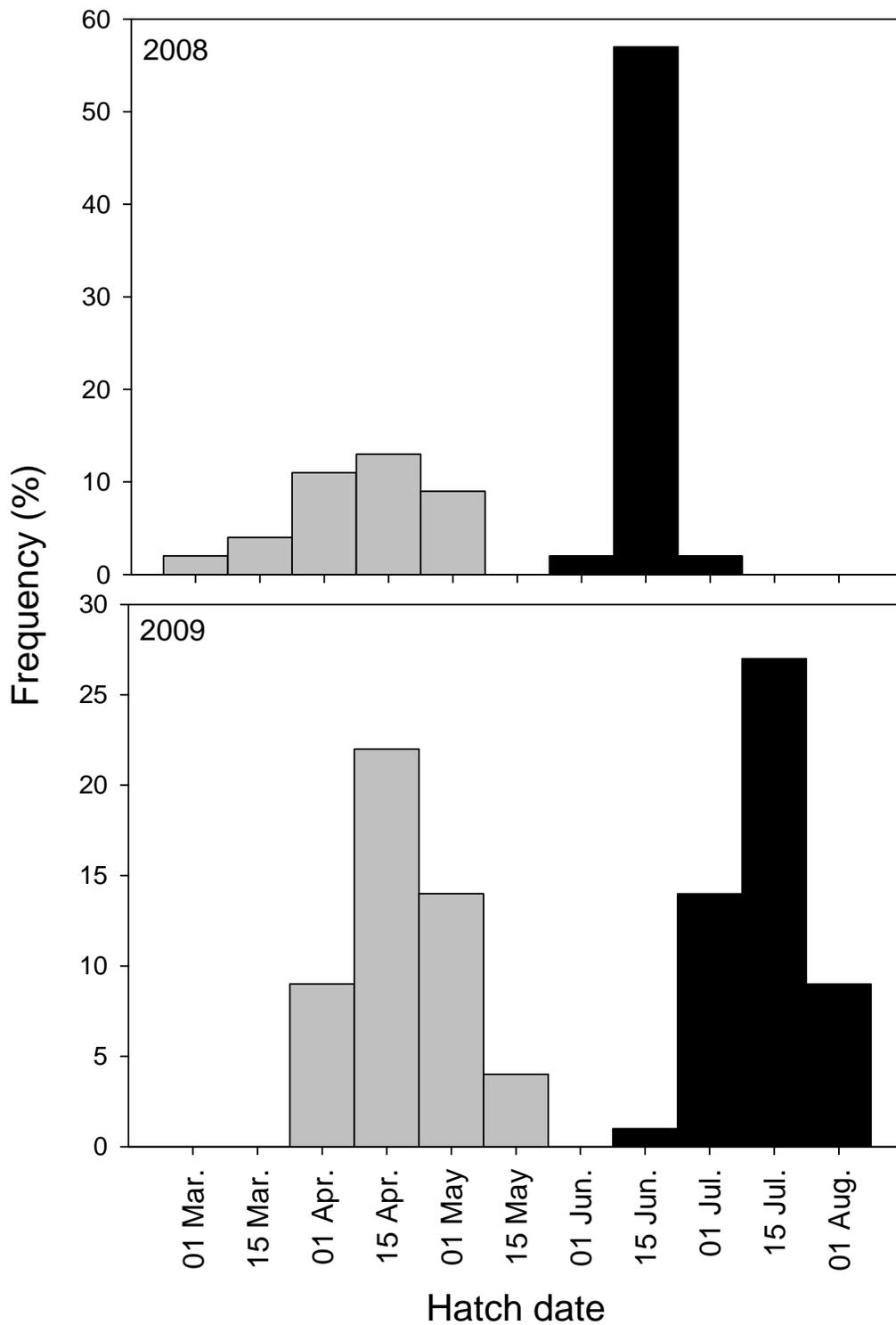
Figure 2.3. Hatch-date distributions of juvenile bluefish. The fish were collected from the Hudson River estuary in 2008 (n = 47, upper panel) and 2009 (n = 40, lower panel). Gray bars represent the spring-spawned cohort and black bars represent the summer-spawned cohort.
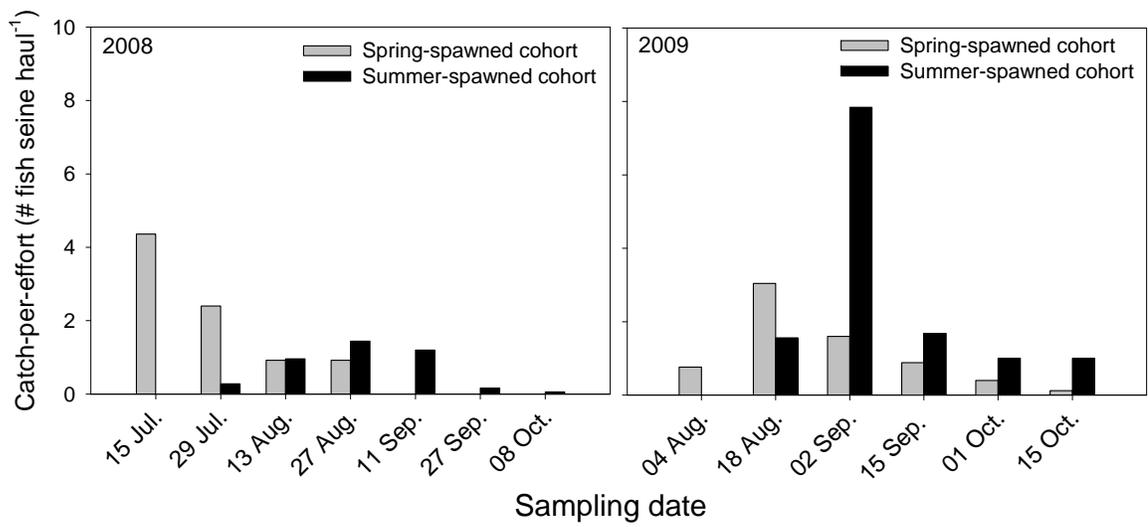
Figure 2.4. Bi-weekly catch-per-effort (CPE) of juvenile bluefish. The fish were collected from the lower Hudson River estuary in 2008 (left panel) and 2009 (right panel).
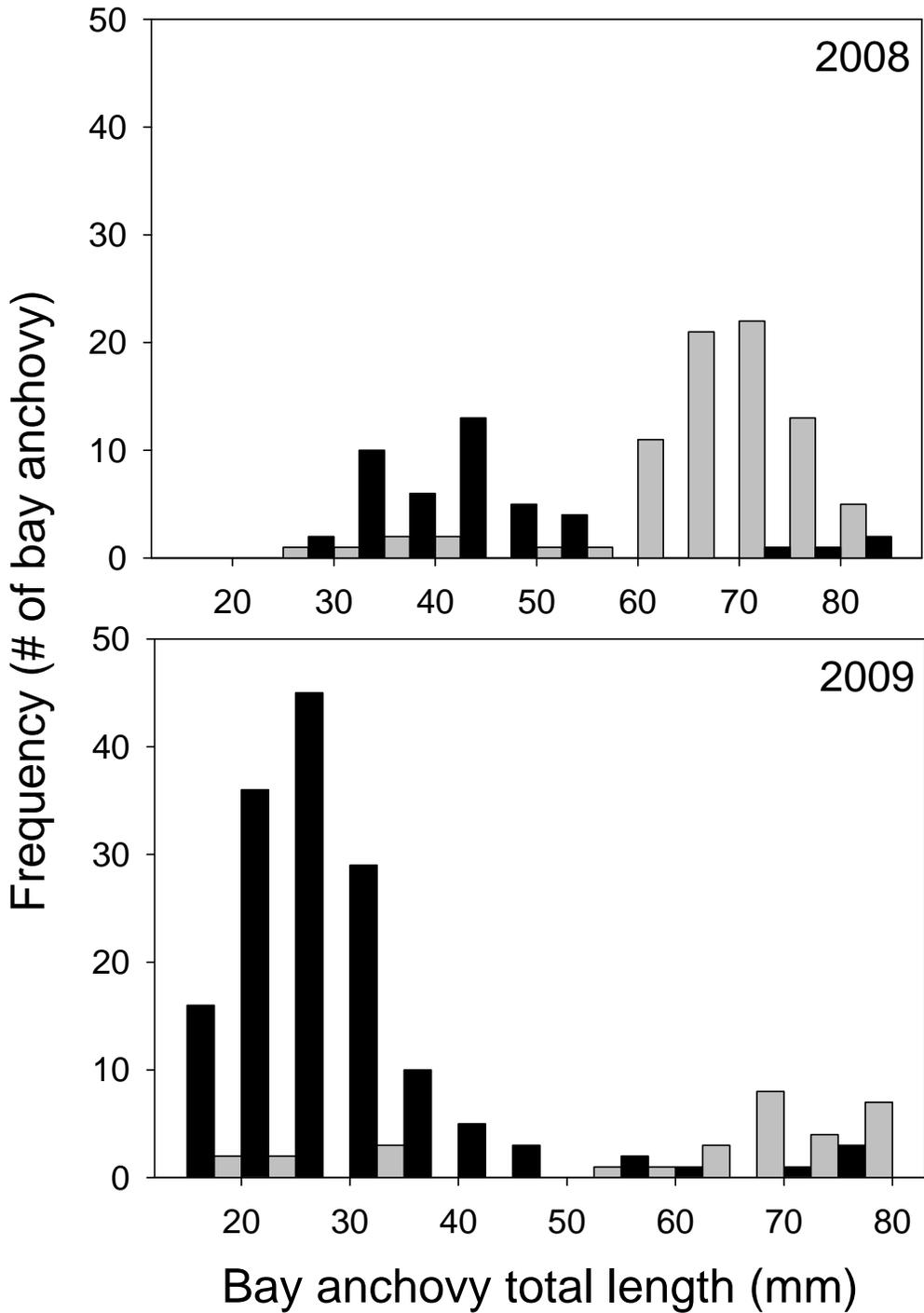
Figure 2.5. Size frequency distribution of bay anchovy found in juvenile bluefish stomachs. Bay anchovy from the stomachs of summer-spawned juvenile bluefish are represented by black bars and from the stomachs of spring-spawned juvenile bluefish by gray bars.
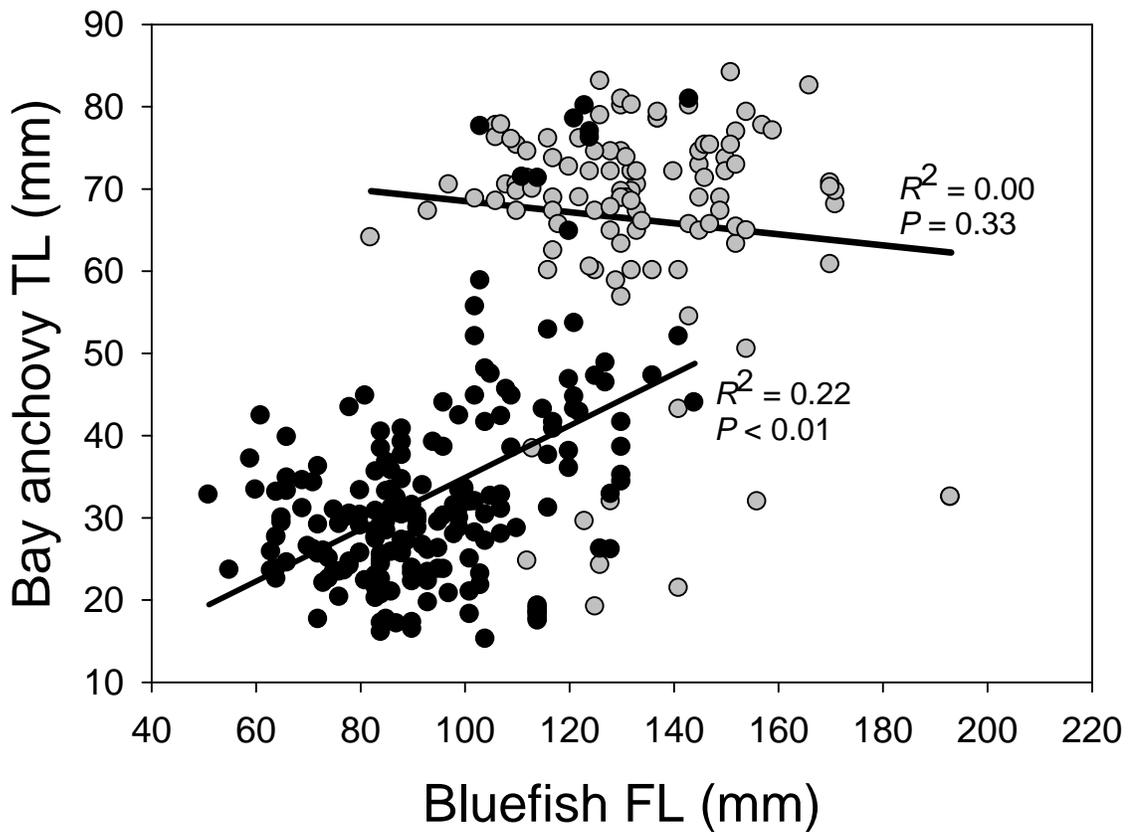
Figure 2.6. Predator to prey size relationships between juvenile bluefish and bay anchovy. The fish were collected from the lower HRE and combined across 2008 and 2009. Black circles represent the sizes of bay anchovy measured from the stomachs of the summer-spawned cohort and gray circles represent the sizes of bay anchovy sizes measured from the stomachs of spring-spawned bluefish.
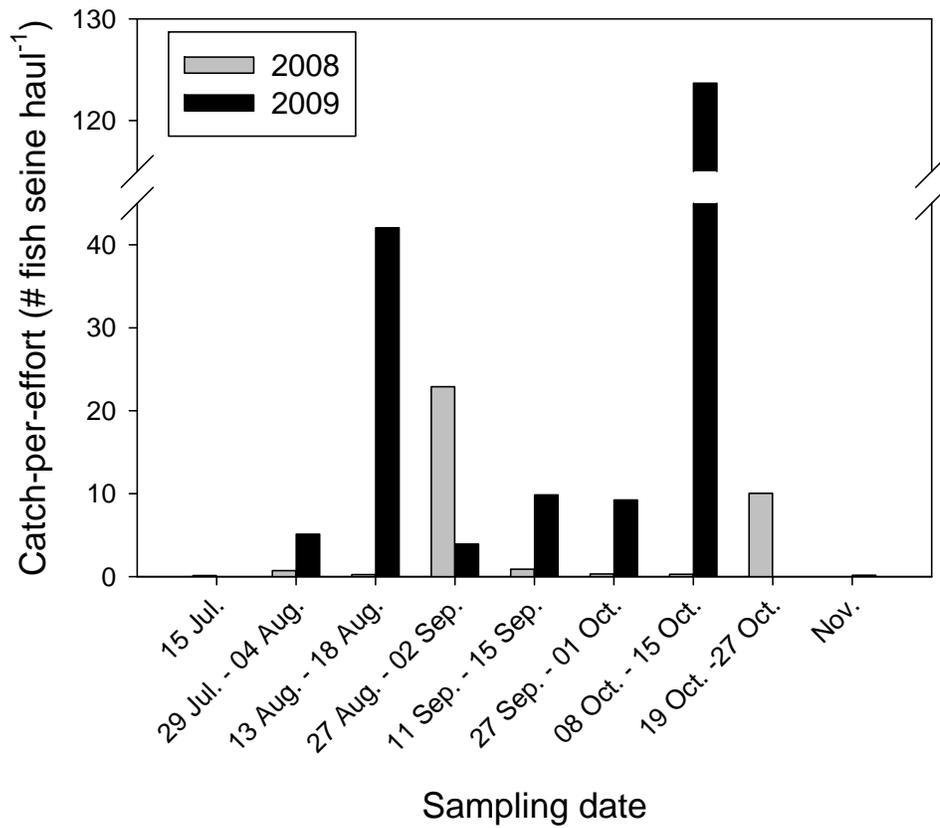
Figure 2.7. Bi-weekly catch-per-effort (CPE) of bay anchovy. The fish were collected from the lower HRE in 2008 and 2009. Each date range corresponds to the sampling dates of closest proximity between the 2008 and 2009 study years.
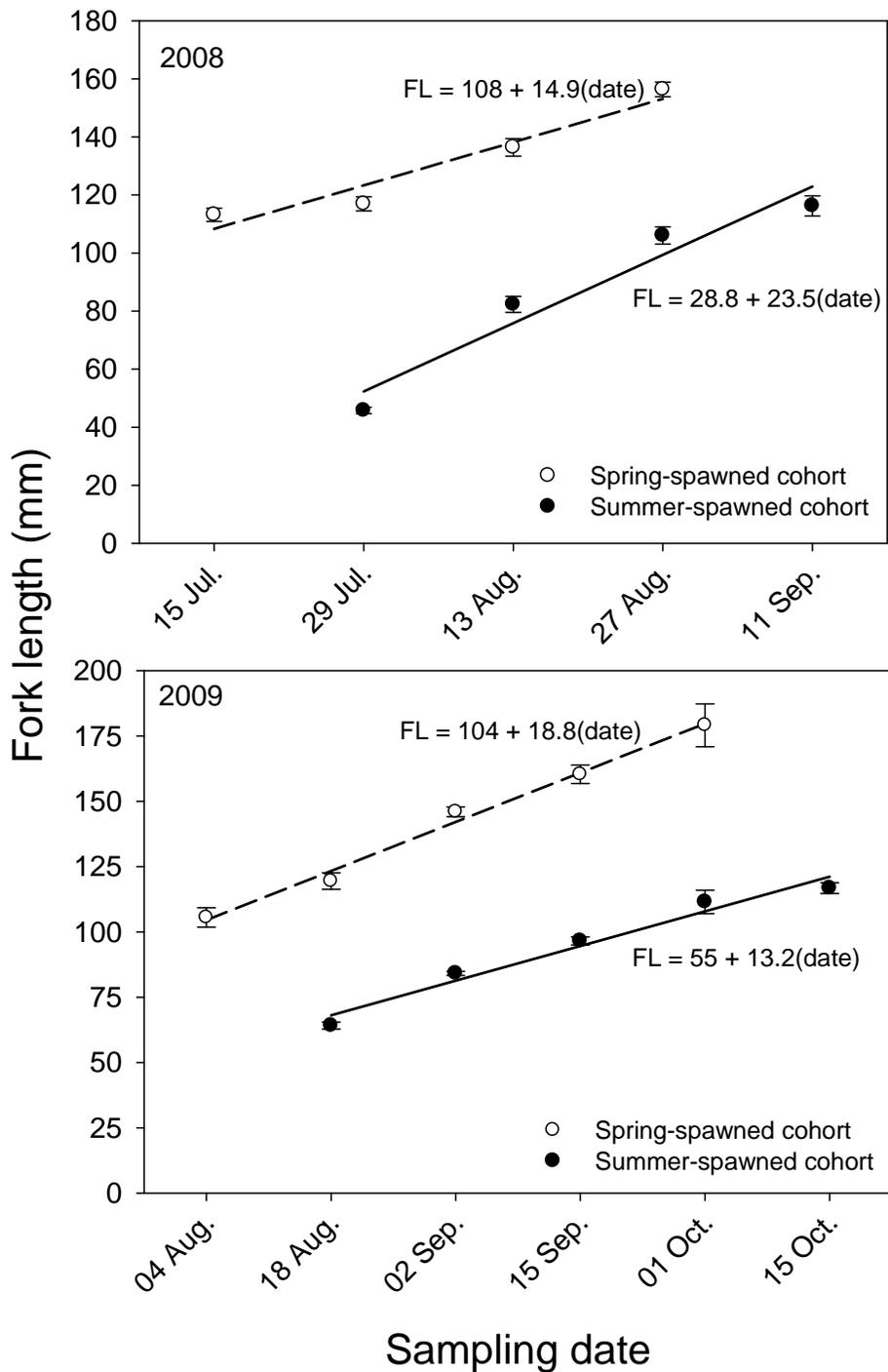
Figure 2.8. Mean fork lengths (FL) and growth rates of the spring- and summer-spawned cohorts of juvenile bluefish. The fish were collected from the Hudson River estuary during the bi-weekly sampling dates in 2008 and 2009.
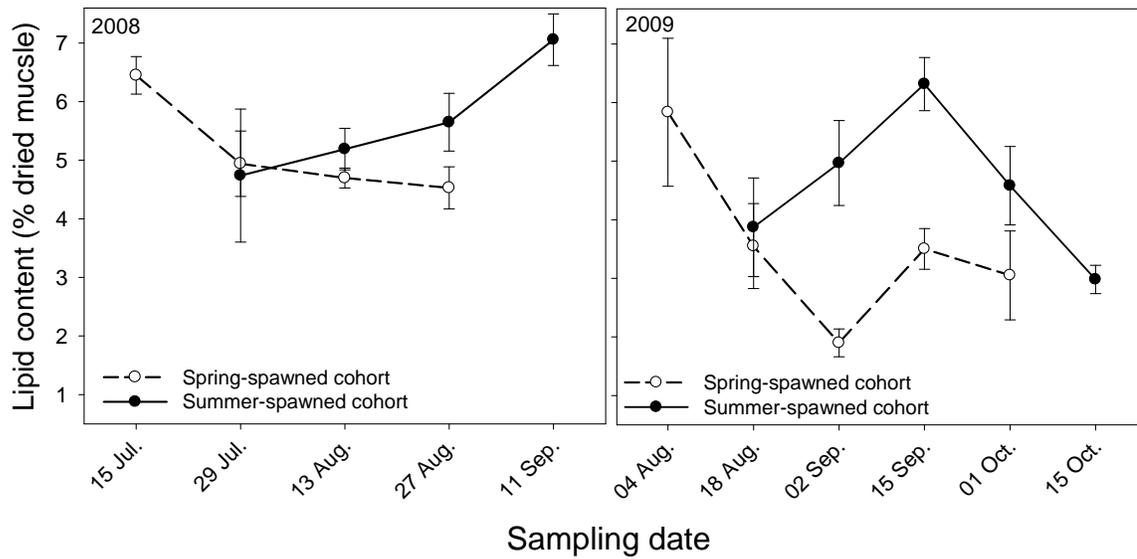
Figure 2.9. Lipid content of spring- and summer-spawned juvenile bluefish. The fish were collected from the lower HRE during the summer and early autumn 2008 and 2009. Error bars represent the standard errors of the cohort-specific lipid content during each bi-weekly sampling period.

CHAPTER 3

OVERWINTER RECRUITMENT, FEEDING BEHAVIOR AND ENERGETICS

OF JUVENILE BLUEFISH IN THE NORTHERN FLORIDA COASTAL OCEAN

3.1 Introduction

For marine fishes that migrate seasonally, juvenile recruitment potential is often

positively correlated with overwinter survival rates (Hurst 2007), and juvenile survival

during winter is partially dependent on habitat quality and prey availability (Griffiths and

Kirkwood 1995; Graeb et al. 2004; Hoxmeier et al. 2004). In marine species that produce

a single cohort of juveniles per year, recruitment success may be vulnerable to stochastic

environmental events, thus increasing annual recruitment variability (Munch and

Conover 2000). Marine fishes that participate in numerous spawning events separated by

space and time produce multiple cohorts of offspring (Potts and Wootton 1984). This

reproductive behavior may result in a dampening of recruitment variability whereby a

single catastrophic biological or environmental event will not destroy an entire year class,

and likely contributes to high juvenile survival (Secor 2007). Multiple spawning events

within a yearly reproductive cycle have been observed in a variety of fishes (Kneib 1993;

Lambert 1984).

One species that produces multiple cohorts of offspring is the bluefish (Munch and

Conover 2000). Bluefish is a highly migratory pelagic species found worldwide in

subtropical, and warm temperate waters (Juanes et al. 1996). Along the United States

coast bluefish occur seasonally in the western Atlantic Ocean from Maine to Florida

(Kendall and Walford 1979) migrating in loosely aggregated schools (Olla and Studholme 1972), and migration timing appears to be regulated primarily by water temperature (Hare and Cowen 1996). In fall, concurrent with decreasing water temperatures, bluefish emigrate from middle Atlantic estuaries and coastal waters, and begin a southerly migration to overwinter in the warmer waters of the South Atlantic Bight (SAB) (Buckel et al. 1999a; Munch and Conover 2000). Much of the research regarding juvenile bluefish ecology has focused on the Middle Atlantic Bight (MAB) and northern SAB during spring, summer, and fall while the southern SAB has received relatively little attention.

Adult bluefish reproduce multiple times along the eastern coast of the United States during annual spawning migrations. Although the exact temporal and spatial patterns of bluefish spawning remain uncertain, at least two cohorts (Kendall and Walford 1979) of juveniles are evident as a result of spawning over the continental shelf (Hare and Cowen 1996). The spring-spawned cohort is produced from bluefish spawning in the SAB from Cape Hatteras, North Carolina to Cape Canaveral, Florida from March to May and the summer-spawned cohort originates from spawning (June – August) along the MAB from Cape Hatteras to Cape Cod, Massachusetts (McBride and Conover 1991).

The relative contribution of the spring- and summer-spawned cohorts to the western Atlantic bluefish population has varied over the last several decades (Juanes et al. 1996; Conover et al. 2003; Taylor et al. 2007). In the 1950s the relative abundance of spring- and summer-spawned cohorts was nearly equal (Lassiter 1962). From the mid-1970s to

the mid-1990s spring-spawned bluefish dominated the cohort demographics of fish inhabiting the MAB (Munch and Conover 2000). However, for reasons unclear, an apparent shift in recruitment has favored the summer-spawned cohort since the mid 1990's (Conover et al. 2003; Wuenschel et al. 2012). This phenomenon may be partially explained by the differential habitat use between the two cohorts.

Juvenile bluefish had been considered estuarine dependent throughout much of the year along the MAB (Chiarella and Conover 1990; Juanes et al. 1996; Able et al. 2003). However, Kendall and Walford (1979) suggested that summer-spawned bluefish might never enter estuaries, instead remaining in the coastal ocean zone during their first summer and autumn. Both spring- and summer-spawned juvenile bluefish used the coastal ocean of New Jersey extensively during summer and early fall (Able et al. 2003), and the summer-spawned cohort has been collected from the continental shelf of Virginia (Gartland et al. 2006) in the fall, and in North Carolina ocean waters throughout the fall and early winter (Morley et al. 2007). The degree of coastal ocean use by juvenile bluefish at the southern extent of the species range in the western Atlantic Ocean is unclear, particularly during winter.

The southern Atlantic coastal ocean zone of Florida may be an under-represented area of potential bluefish recruitment especially during winter. The Florida Current along the east coast of the state during the winter produces a complex coastal temperature band which causes a steep latitudinal thermal gradient. The absence of the Florida Current on the Gulf coast results in warm winter water temperatures on the east coast of the state

(Gilmore and Hastings 1983). This latitudinal thermal environment during winter along the Florida east coast creates a sub-tropical aquatic environment for the fish fauna inhabiting what have been defined as temperate waters. Juanes et al. (2013) showed that Florida estuaries provided juvenile bluefish with higher prey abundances and more favorable water temperatures than nursery areas in the MAB during winter, but collected few summer-spawned individuals. The coastal shelf was not sampled in their study, but it was suggested that this area may be inhabited throughout winter by summer-spawned juvenile bluefish.

The National Marine Fisheries Service (NMFS) conducts extensive spring and autumn surveys that cover much of the continental shelf from Cape Hatteras to the Gulf of Maine. However, the region from Cape Hatteras, North Carolina south to Florida is not sampled by this survey, nor is the shallow coastal zone (<10 meters) due to the depth requirements of the survey ships. Further, the Southeast Area Monitoring and Assessment Program (SEAMAP), a State/Federal/university program that collects fishery-independent data from shallow nearshore waters of northeastern Florida does not sample during the winter. The importance of inner-continental shelf waters to bluefish during winter requires attention to achieve a more complete recruitment index. In fact, the importance of quantifying essential habitats for economically important fishes including bluefish is underscored by NOAA's Essential Fish Habitat Program. The purpose of this study was to evaluate the role of the coastal ocean shelf of northern Florida to juvenile bluefish by measuring cohort-specific winter abundance, feeding behavior and lipid content.

3.2 Materials and methods

3.2.1 Study area and fish sampling

Four sites located along the U.S. Atlantic coastal shelf between St. Augustine and New Smyrna Beach, Florida were sampled monthly during late fall through winter 2006/07, and 2007/08 (Figure 3.1). February sampling was not conducted in both years. The 4 sites were spaced latitudinal, approximately 30-35 Kilometers (km) apart and depth-stratified; the shallow strata ranged from 5-9 meters (m) and the deep strata from 10-18 m. Sites were selected based on an associated study that incorporated co-located surf zone and estuarine sampling, and were numerically defined 1-4 from north to south. At all 4 sites, inner-continental shelf sampling encompassed the area just outside of the surf zone to 5 km offshore, and consisted of mud to sand bottom.

Site 1 was located outside of the Tolomato River and Saint Augustine Inlet in St. Johns County and served as the northern site (Figure 3.1). Heavy coastal development, channel dredging, and boat traffic further defined the coastal shelf outside of the St. Augustine Inlet as the highly disturbed estuarine site. Site 2 was the coastal ocean outside of the Matanzas River Inlet also in St. Johns County and extended south into northern Flagler County. The Matanzas Inlet is one of the last natural inlets on Florida's east coast and has remained unaltered with no dredged channel or armored shoreline and represented the undisturbed site. Site 3 was the coastal ocean offshore of Flagler Beach in Flagler County. The Flagler Beach site was selected for comparative purposes because it was located within the study area, but was the only site not associated with an estuary. The inner-continental shelf area outside of the Ponce Inlet, New Smyrna Beach in Voulusia

64

County represented the southernmost site (4). Ponce Inlet is the main channel for boats traveling between the Atlantic Ocean and the Halifax and Indian Rivers. This site is characterized by two jetties at the mouth of the inlet and it has undergone several dredging events for safe inlet navigation. The Ponce Inlet was further defined as the moderately disturbed site.

Ocean trawling was conducted with a commercial shrimp trawling vessel. Juvenile bluefish were collected from inner-continental shelf habitats (≤18 m) with a bottom otter trawl (30 m head rope, 6 mm codend), towed at 3 knots for 20 minutes (min). Two trawls were towed per depth strata at each site (total = 16 tows per month) during daylight hours. Trawling commenced approximately 1 hour (hr) after sunrise and terminated 1 hr after sunset and was separated into three time periods (morning: first tow – 12:00 pm; afternoon: 12:01 pm – 5:00 pm; evening: 5:01 pm - last tow). For all sampling efforts, collected fishes were processed on deck, measured immediately and selected samples of juvenile bluefish were preserved (95% EtOH or frozen) for stomach content analysis. For each tow, numbers of all species captured were estimated by direct counts or gravimetrically, and a sub-sample was enumerated, measured, and returned to the water as quickly as possible in order to minimize mortality.

3.2.2 Ocean temperature

Sea surface temperature was recorded at the beginning of each trawl using the ship's depth finder. The monthly ocean temperatures were similar between years and combined

during subsequent analysis. Differences in monthly ocean temperature were assessed with a one-way analysis-of-variance (ANOVA).

3.2.3 Cohort classification

In the laboratory, individual juvenile bluefish were measured to ± 1.0 millimeter (mm) fork length (FL) and total length (TL), and weighed (± 0.1 grams (g) wet weight). Juvenile bluefish cohort-specific abundances were determined by length-frequency analysis for each sampling month. All bluefish < 350 mm FL were designated as age-0 juveniles (Wuenschel et al. 2012), and independent cohorts were considered present if distinct size groups were evident. Fishes that coincided with these groupings were assigned to spring (< 350 mm FL; October – November) -, summer (< 250 mm FL; December – January) -, and fall (< 150 mm FL; January, < 250 mm FL; March) - spawned cohorts respectively based on juvenile bluefish age and growth in this region (Murt and Juanues 2009). In months where juvenile bluefish were collected from more than 1 cohort, the antimode in length (mm) distributions was used as the boundary between cohorts.

3.2.4 Spatial and temporal recruitment dynamics

To reveal spatial and temporal recruitment dynamics to the region catch-per-effort (CPE) was compared between years with a paired t-test. Catch rates were similar between years and combined during subsequent analyses. Catch-per-effort was compared among cohorts, stations, and months with a three-way ANOVA, and between depth strata with a t-test. Catches of juvenile bluefish were log (x+1) transformed to meet the assumptions

66

of parametric statistical analyses and Tukey's multiple comparison tests were used to evaluate pair-wise differences in CPE between the independent variables. Catch rates of juvenile bluefish during the time periods were non-normally distributed after transformation and analyzed with a Kruskal-Wallis non-parametric test on ranks and a Dunn's multiple comparison evaluation.

3.2.5 Diet composition

The stomach was extracted from each juvenile bluefish and all contents removed from the esophagus to the pylorus. Each stomach was opened, and the inner walls scraped with a scalpel to remove any remaining contents. Diets were enumerated, identified to the lowest possible taxon, blotted dry, and weighed (±0.001 g wet weight). Whole prey fishes were measured to total length (±0.10 mm). Results for each prey taxon were reported as percent frequency of occurrence (%FO; the number of stomachs in which a prey type occurred expressed as a frequency of the total number of stomachs in which prey were present), percent composition by wet weight (%W; the total weight of that taxon expressed as a percentage of the total stomach content weight), and percent composition by number (%N; the number of individuals of that taxon expressed as a percentage of the total number of prey). Prey items were considered important if they contributed >10% in any of the calculated indices.

3.2.6 Feeding behavior

The frequency of empty bluefish stomachs was compared among months and stations, and between years, time periods and cohorts using chi-square goodness of fit tests (SAS

2009). November was excluded from comparison because fish were not returned to the laboratory during this month. For juvenile bluefish that contained food, feeding intensity (FI) was calculated as a proportion of prey weight to bluefish body weight:

$$(FI = FSW - ESW/GW)$$

Where FSW is the stomach weight with contents, ESW is the empty stomach weight, and GW is the gutted bluefish weight (all in g). Temporal and spatial differences in feeding behavior were examined by comparing FI between years and depths with t-tests and among months, stations, and time periods with ANOVA. If a significant interaction was detected, a Bonferroni correction ($P = 0.05/N$) was applied to account for the pair-wise type I error rate, where N was equal to the number of comparisons.

The relationship between juvenile bluefish size and prey size was examined using least squares linear regression analysis. Relative prey size was calculated by dividing individual prey TL by bluefish TL and the relationship between relative prey size and juvenile bluefish size was examined by calculating Spearman's rank order correlation coefficients (r_s). For juvenile bluefish with stomachs that contained partial, but identifiable remains of dominant prey, otolith lengths (OL mm) from vouchers of identified prey collected at the time of bluefish sampling were used to reconstruct whole prey length (TL). Striped anchovy (*Anchoa hepsetus*) represented the only dominant prey species found in the stomachs of juvenile bluefish and the linear regression used for reconstructing whole prey size was calculated as:

$$TL = 30.33 + (12.35 * OL), n = 83, R^2 = 0.53, P < 0.0001$$

Reconstructed whole prey size was compared to intact whole prey size in juvenile

bluefish stomachs using the Mann-Whitney Rank Sum Test.

To evaluate juvenile bluefish prey type selectivity, relative prey abundance in the

sampling area was calculated using trawl by-catch data, and was computed as the number

of each species collected per tow. Bluefish prey selectivity was calculated using the

Manly-Chesson (1983) index:

$$\alpha_i = \frac{(r_i / p_i)}{\sum\limits^{m} (r_j / p_j)} , i = 1, \ldots, m,$$

where α_i is the selectivity for prey type i, r_i is the relative abundance of prey type i in

bluefish stomachs, p_i is the relative abundance of prey type i in the study area, and m is

the total number of prey species in the study area. Random feeding occurs when $\alpha_i = 1/m$.

A value of $\alpha_i > 1/m$ indicates that the prey species is selected, and if $\alpha_i < 1/m$, the prey

species is avoided. The selectivity index was calculated using the relative abundance of

only those individuals that were within the size range of prey consumed by juvenile

bluefish and occurred with juvenile bluefish in the study area.

3.2.7 Lipid content

To determine lipid content, approximately 2-4 grams (g) of white muscle was removed

from individual juvenile bluefish. White muscle was selected for lipid content analysis

because this tissue is an appropriate proxy for overall energy content of juvenile bluefish

(Slater et al. 2007). Tissue samples were weighed (± 0.001 g) and dried at 60 ºC for 72

hours. An automated soxhlet extractor with di-ethyl ether was used to dissolve neutral

lipids with a method similar to Shahidi (2001). The post-extracted muscle samples were

dried at 60 ºC for 24 hours to ensure evaporation of any remaining solvent.

Lipid levels of juvenile bluefish were expressed as a proportion of the sample dry weight

and arcsine square root transformed prior to analysis due to non-normality and

heterogenous variances. Lipid content was compared between years with a t-test and

among months using ANOVA and post-hoc Tukey's multiple comparison tests to

determine pair-wise differences in monthly lipid content. Muscle tissue samples were not

available for fish collected in November, so this month was omitted from the lipid

content analysis. All analyses were performed using SAS 9.3 software (SAS Institute,

Cary, N.C.)

3.3 Results

3.3.1 Water temperature

Monthly water temperatures were similar among the 4 sampling stations, and between

years ($P > 0.05$). Seasonal ocean temperatures for all 4 stations and years were

subsequently combined (Figure 3.2) and ranged from 15.5°C in January to 28.4°C in

October. In both years, ocean temperature was warmest in October (mean = 27.7°C).

Monthly water temperatures decreased from October to December and were lowest in

January (mean = 19.1°C; Figure 3.2). By March, the mean ocean temperature increased

to 20.4°C (range = 19.9-21.0°C).

3.3.2 Spatial and temporal recruitment dynamics

A total of 1,143 juvenile bluefish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08: 44 at site 1, 166 at site 2, 592 at site 3, and 341 at site 4. Spatially, the pattern of juvenile bluefish abundance among the 4 sites was similar between years ($P > 0.10$), and subsequently combined across years. Catch-per-effort was highest at site 3 (Flagler Beach) and lowest at site 1 (St. Augustine) ($F = 3.1$, d.f. $= 3$, $P = 0.03$; Figure 3.3a). Catch rates of juvenile bluefish were also 2 times greater in the deep (10-18 m; CPE $= 14$ fish/tow) strata than in the shallow (5-9 m; 7 fish/tow) transects ($t = 2.4$, $P = 0.05$).

Catch-per-effort of juvenile bluefish to the northern Florida coastal region differed among months ($F = 2.8$, d.f. $= 4$, $P = 0.03$). Catch rates were lowest in October (CPE $= 0.44$ fish/tow; Figure 3.3b), and juvenile bluefish were collected at only the 2 northern-most sites during this month. Monthly CPE increased throughout the winter and peaked in January (CPE $= 28$ fish/tow). Catch-per-effort in January was at least 5 times greater than in any other month, and juvenile bluefish inhabited all 4 stations during this month. By March, catch rates declined from January, but were higher than observed during autumn and fish were collected at all sites except for site 1 (Figure 3.3b). Catch rates of juvenile bluefish increased from morning to afternoon, but declined to the lowest levels during the evening time period ($H = 15.6$, d.f. $= 2$, $P < 0.01$; Figure 3.3c).

3.3.3 Cohort-specific recruitment dynamics

Juvenile bluefish recruitment to the northern Florida coastal ocean was represented by spring-, summer-, and fall-spawned cohorts. Overall, CPE was highest for the summer-spawned cohort, and lowest for spring-spawned juvenile bluefish (F = 5.93, d.f. = 2, P < 0.01). Catch rates were more than 9 times higher for summer-spawned juvenile bluefish than either the spring- or fall-spawned cohorts (Figure 3.3d).

Cohort-specific CPE was similar between years but varied among months, sites, time periods, and depth strata (Table 3.1). The entire catch of juvenile bluefish in October, and November was represented by the spring-spawned cohort, while in December only summer-spawned bluefish were collected. In January, CPE was highest for the summer-spawned cohort, and by March the fall-spawned juvenile bluefish dominated catches of juvenile bluefish (Table 3.1). Catch rates of summer-spawned bluefish were highest among the 3 cohorts at all stations, depth strata, and time periods (Table 3.1).

Length frequency analysis showed that the spring-spawned cohort migrated to the northern Florida coastal ocean in October (mean FL = 279 mm; range = 245-336 mm FL), but individuals of this cohort were not captured after November (Figure 3.4). Cohort-specific analysis showed that no spring-spawned juvenile bluefish were captured during evening trawls, and CPE was similar during the morning and afternoon (Table 3.1). Catch rates of the spring-spawned cohort were highest at the most southern site 4 (Ponce inlet), and similar between depth strata (Table 3.1).

Summer-spawned juvenile bluefish first appeared in December (mean FL = 182 mm; range = 117-270 mm FL), and CPE was highest in January (Table 3.1). Afternoon was the time period of greatest catches, while few juvenile bluefish were collected during the evening. Spatially, CPE was highest at site 3 (Flagler), and lowest at site 1 (St. Augustine), but summer-spawned juvenile bluefish inhabited all 4 sites in this region during January sampling. Catches of summer-spawned juvenile bluefish were greater in the deep strata than in shallow transects (Table 3.1).

During January in both years, the fall-spawned cohort recruited to the study area and dominated juvenile bluefish recruitment during March (mean FL = 180 mm; range = 25-224 mm FL). Catch-per-effort of fall-spawned juvenile bluefish was highest during morning and no individuals of this cohort were collected during any evening trawls. Similar to the summer-spawned cohort, CPE of fall-spawned juvenile bluefish was greatest at site 3. However, unlike the spring- and summer-spawned cohorts, fall-spawned fish were more common in the shallow strata (Table 3.1).

3.3.4 Diet composition

Diet composition was described from 434 juvenile bluefish caught in the northern Florida coastal ocean. The total lengths of juvenile bluefish ranged in size from 86 mm – 300 mm TL (mean TL = 210 mm). Prey items were found in 54% of all the stomachs processed. A total of 327 prey items were found, 87% of which were identifiable. Of the identifiable prey items, only 5 taxa were present. Four of the 5 taxa were fishes. Prey

items were categorized into 4 primary groups; (1) striped anchovy (*Anchoa hepsetus*), (2) all other fish, (3) unidentified fish remains, and (4) squid.

Overall, striped anchovy was the most important source of food for juvenile bluefish in the northern Florida coastal ocean during late fall and winter 2006/07 and 2007/08. Striped anchovy occurred in 64 % of the stomachs that contained prey, and dominated the diet composition by weight and number (Table 3.2). Unidentified fish remains constituted the second dominant prey group, and all other fish contributed less than 10% to the diet of juvenile bluefish. Squid were the only invertebrate found in bluefish stomachs, but did not contribute more than 5% to the diet in any of the indices (Table 3.2). No evidence of cannibalism was found.

Differences in the diet composition of juvenile bluefish were evident between years. Striped anchovy contributed less to the diet of juvenile bluefish in 2006/07 than in 2007/08, but were still the most important prey species in both years (Table 3.2). This difference in diet composition of juvenile bluefish between years was associated with the proportion of unidentified fish remains. Unidentified fish remains were found in 43% of juvenile bluefish stomachs in 2006/07, and only 9% of stomachs in 2007/08. Of the other fish species found in juvenile bluefish stomachs, Atlantic thread herring (*Opisthonema oglinum*) was present only in 2006/07, whereas Atlantic bumper (*Chloroscombrus chrysurus*) was found exclusively in 2007/08 (Table 3.2).

The only prey groups included in the prey selectivity index were those with relative abundance contributions in the study area >1% in each sampling period and with individual total lengths ≤ 50% of juvenile bluefish size (TL). Ten prey groups met these criteria and were considered available to juvenile bluefish throughout the study period; 9 fish groups and 1 invertebrate group. Only the results of the prey consumed by juvenile bluefish are shown in Figure 3.5. The five other abundant prey groups available to, but not consumed by juvenile bluefish during the study period and in order of highest relative abundance in the study site were lookdown (*Selene vomer*), family Sciaenidae (not identified to species), moonfish (*Mene maculate*), Atlantic butterfish (*Peprilus triacanthus*) and harvestfish (*Peprilus paru*). Juvenile bluefish exhibited strong positive selection for striped anchovy ($\alpha = 0.63$), non-selective feeding on Atlantic cutlassfish (*Trichiurus lepturus*) ($\alpha = 0.19$), and avoidance of the 3 other prey groups (Figure 3.5).

3.3.5 Feeding behavior

The frequency of empty stomachs differed between years, and among months, time periods, stations, and cohorts ($\chi^2 = 13.2 – 72.1$, P < 0.005; Table 3.3). In 2006/07, 77% of juvenile bluefish stomachs were empty, compared to 35% in 2007/08. The frequency of empty stomachs was similar among months, time periods, stations and cohorts within each year and subsequently combined across years. The occurrence of empty stomachs was lowest in December (40%) and highest in March (83%). More juvenile bluefish had empty stomachs during the afternoon (81%) than in the morning (45%), and evening was excluded from the comparison due to a low sample size of fish with diet contents collected during this time period. Spatially, the frequency of empty stomachs was similar

between juvenile bluefish inhabiting the deep (51%) and shallow (46%) depth strata. The

highest proportion of empty stomachs was observed at site 3 (88%) while only 30% of

juvenile bluefish collected at site 1 didn't contain prey. The spring- and summer-

spawned cohorts of juvenile bluefish had a similar and lower number of empty stomachs

than the fall-spawned cohort (84.8%; Table 3.3).

The feeding intensity of juvenile bluefish was greater in 2007/08 than in 2006/07 ($P <$

0.01; Figure 3.6a). Relative stomach fullness was also higher in winter months than

during October and March ($P < 0.01$; Figure 3.6b), and no interaction between month and

year was detected. Feeding intensity was similar between the morning and afternoon

(Figure 3.6c). Spatially, the highest feeding intensity of juvenile bluefish was observed at

site 4 ($P < 0.01$; Figure 3.6b), and in shallow strata ($P < 0.001$; Figure 3.6e). The

summer-spawned cohort exhibited greater feeding intensity than the spring- and fall-

spawned cohorts ($P = 0.03$; Figure 3.6f).

Regression analysis showed no linear relationship between juvenile bluefish length and

prey length ($\beta = 0.03$, $\alpha = 50.21$, $R^2 = 0.002$, $n = 197$, $P = 0.21$; Figure 3.7). Prey sizes

ranged from 16 mm – 177 mm TL (mean = 57 mm TL). Striped anchovy comprised 91%

of the prey for which measurements were available. Juvenile bluefish consumed striped

anchovy between 47 – 79 mm TL (mean = 56 mm TL). Size reconstruction of partially

consumed striped anchovy from the otolith length to TL relationship resulted in the size

determination of 82 additional prey. The reconstructed TL of partially consumed striped

anchovy were larger than whole fish in the stomachs of juvenile bluefish (U = 3038.0, P

= 0.04) indicating a different feeding strategy for larger prey. Atlantic bumper, Atlantic thread herring and squid constituted only 6.6% of the prey for which measurements were available, but represented the 11 smallest prey consumed (Figure 3.7). Atlantic cutlassfish were the largest prey consumed by juvenile bluefish (n = 5; mean = 151 mm TL). Relative prey size was not related to juvenile bluefish size (r = -0.13; n = 197; P = 0.06). The calculation of relative prey sizes indicated that juvenile bluefish typically consumed prey approximately 25% of their TL, but ranged between 8.0% - 84.0%. Relative prey sizes were largest in juvenile bluefish that consumed Atlantic cutlassfish (mean = 64%), and smallest for fish that preyed upon Atlantic bumper (mean = 13%).

3.3.6 Lipid content

The monthly lipid content of juvenile bluefish was similar between years, but showed clear seasonality, with a significant effect of month during the study duration (F = 3.60, P = 0.02, n = 57). Proximate lipid content was lowest in October and increased throughout the winter before declining in March (Figure 3.8). Due to the cohort-specific monthly migration to the region, the differences in lipid content among months also represented differences in energetics among the three cohorts, such that only spring-spawned fish were collected in October, while summer-spawned fish were collected in December and January, and March caught fish represented the fall-spawned cohort. Summer-spawned juvenile bluefish contained five times greater white muscle lipid content (mean = 2.5%) than the spring-spawned cohort (mean = 0.5%), and January caught summer-spawned fish had twice the lipid content of the fall-spawned cohort (mean = 1.4%; Figure 3.8).

3.4 Discussion

3.4.1 Spatial and diurnal recruitment dynamics

Throughout the study period, juvenile bluefish were collected from all four sites, but CPE was highest at site 3 (Flagler Beach). Interestingly, Flagler Beach represented the only site that was not associated with a coastal estuary, providing evidence for the importance of oceanic waters to juvenile bluefish. Catch rates of juvenile bluefish were lowest at the St. Augustine site. We classified the St. Augustine location as the most altered site due to a variety of activities including channel dredging, jetty construction and coastal development. These activities can disturb bottom sediments resulting in increased turbidity, and may interfere with the foraging ability of fish. Further, the effluents from coastal development have been shown to contain higher concentrations of toxic substances than already in the water column (Hoffman et al. 1984). We also observed heavy boat traffic at this site throughout the winter. Although the effects of such activities on bluefish behavior are unclear, CPE was more than twenty times lower at this site than at the less trafficked Flagler Beach site. Juvenile bluefish may have avoided or been displaced from the nearshore area around the St. Augustine inlet in favor of the less altered locations along the northeast Florida coast. An alternative explanation for the low abundance observed of juvenile bluefish in the St. Augustine region could be that this site was located at the highest latitude and bluefish may have continued south after arriving to the region. A latitudinal gradient in abundance was evident and cannot be discounted as a factor influencing the distribution of juvenile bluefish as winter water temperatures declined. A comparison of the community composition among the four stations would

elucidate the spatial ecology of overwintering fishes in the region, and should be the focus of future work.

This study presented the unique opportunity to examine juvenile bluefish coastal shelf distribution in depths from 5 – 18 m, and to our knowledge, the first attempt to do so during winter at the southern extent of the species range in the U.S. We found that juvenile bluefish were more abundant in the deep strata than in the shallow transects. Selection for depths greater than 9 m appears to be unique for juvenile bluefish. Able et al. (2003) reported higher juvenile bluefish abundance in depths less than 10 m than depths from 11 – 30 m along the New Jersey coast during summer and early fall. Our results showed that the summer-spawned cohort of juvenile bluefish selected depths between 10 - 18 m throughout winter along the northern Florida inner continental shelf, and this area should be considered as essential juvenile bluefish habitat in this region.

Within our study area, juvenile bluefish were most abundant in the afternoon. Catch rates were three times greater in the afternoon than the morning, and only 1 juvenile bluefish was collected during evening trawls. The increased diurnal activity observed here is consistent with previous studies of juvenile bluefish movement in MAB estuaries (Juanes and Conover 1994; Able et al. 2003). In the Hudson River estuary, juvenile bluefish inhabited shoreline areas during the day and moved offshore at night (Buckel and Conover 1997). The pattern of increasing abundance from the morning to the afternoon and to deeper water that we observed for juvenile bluefish inhabiting the northern Florida coastal ocean indicates that these fish may move to offshore waters at night.

3.4.2 Temporal recruitment patterns

Several aspects of coastal marine systems differ from other habitats to overwintering fishes, most notably the lack of isolating barriers. Open population boundaries allow fish to adopt migration strategies which may reduce exposure to thermal stress (Hurst 2007). Many marine fishes that inhabit non-boundary coastal waters migrate long distances prior to or during winter to maximize survival, as winter can be a period of increased mortality (Able and Fahay 1998). The temporal pattern of juvenile bluefish recruitment to the coastal waters of northern Florida appeared to be related to ocean temperatures. Juvenile bluefish typically leave MAB estuaries, joining with individuals in the surf zone and coastal shelf to make a southerly migration to overwintering habitats as water temperatures fall below 15 °C (Juanes et al. 1996). The northern Florida coastal ocean appeared to provide juvenile bluefish with an adequate thermal refuge during the winter as mean daily temperatures in the sampling area were consistently above 20°C and never fell below 15°C.

In October and November, average daily ocean temperatures in our sampling area were above 25°C. Hartman and Brandt (1995) showed that juvenile bluefish growth slows at temperatures greater than 24°C as a result of increased metabolic demands. In the present study, catch rates of juvenile bluefish were lowest during these two months, suggesting that individuals were just beginning to arrive to the region. Juvenile bluefish occurrence during October and November has been reported as far north as New York and New Jersey (Juanes et al. 1993; Able et al. 2003; Taylor et al. 2007), and abundance in October was shown to be highest in coastal North Carolina during the cooler autumn of a

80

2 year study (Morley et al. 2007). It is likely that ocean temperatures farther north in the MAB were cooler than in Florida coastal waters during October and November providing suitable habitat for juvenile bluefish to maximize growth potential.

As ocean temperatures declined in December, juvenile bluefish CPE increased along the northern Florida coastal shelf. Although the change in ocean temperature was greatest between November and December, declining approximately 4.5°C to a monthly mean of 20.6°C, the daily ocean temperatures experienced by bluefish inhabiting the northern Florida coastal ocean in December were well above what has been considered the low temperature tolerance for the species (13-15°C, Hare and Cowen 1996). If water temperatures to the north decreased similarly, juvenile bluefish would have been forced to move to warmer waters such as those provided in the northern Florida coastal ocean during this study. Recruitment of juvenile bluefish to nearshore oceanic waters along the North Carolina coast were high in December during the warmer winter of a two year study, but declined considerably in December during the colder winter (Morley et al. 2007). December could represent a transitional period along the SAB such that inter-annual water temperatures during this month oscillate around 14°C in northern regions, but are consistently above the minimum temperature tolerance of juvenile bluefish in the southern SAB.

Monthly ocean temperatures along northern Florida coastal shelf were coldest in January, but juvenile bluefish abundance was highest during this month in both years of the study. This study represented the first examination of juvenile bluefish recruitment in which

regional abundance was greatest during January. The coldest ocean temperatures were recorded in January, but did not fall below 15°C during the sampling period and were consistently above 20°C. Morley et al. (2007) showed that young-of-the-year (YOY) bluefish disappeared from North Carolina coastal waters in January as Atlantic Ocean temperatures declined to 9°C and suggested a southward or offshore migration as two possible explanations for the emigration of bluefish from their study site as ocean temperatures declined. Our results showed that a southward migration likely explained the movement of juvenile bluefish away from MAB and northern SAB waters during the coldest months of the year.

Catch rates of juvenile bluefish declined from January to March. Juanes et al. (2013) reported a decline in water temperatures to 9°C during February in northern Florida estuaries, and didn't collect any juvenile bluefish during this month. Although February sampling was not conducted during the present study, a post hoc examination of sea surface temperatures recorded by the NOAA buoy #SAUF1 (29°51'24"N, 81°15'54"W) located in the coastal ocean off of St. Augustine Florida showed that the mean 2007/2008 February water temperature was 15.4°C. This temperature was warmer than the associated estuary and above the lower thermal tolerance of juvenile bluefish (Hare and Cowen 1996), confirming the notion that the northern Florida coastal ocean provides a thermal refuge for juvenile bluefish over the winter season. During March, water temperatures in our study area increased to 20.4°C. Morley et al. (2007) did not collect any juvenile bluefish during March from North Carolina waters in both years of a two year study. March sea surface temperatures in the MAB and northern SAB were likely

below the range of temperatures selected by juvenile bluefish, but within the species thermal optima along the northern Florida coast.

3.4.3 Cohort-specific recruitment patterns

We collected 3 cohorts of juvenile bluefish in the coastal ocean of northern Florida, providing support for the recognition of this region as important overwinter habitat. In October and November, only individuals of the spring-spawned cohort were collected. Spring-spawned juvenile bluefish typically emigrate from MAB waters approximately one month earlier than their younger con-specifics (McBride et al. 1995). Wuenschel et al. (2012) showed that catches of the spring-spawned cohort declined in the northern regions (New York and New Jersey) during August and early September, but appeared during late September sampling in Maryland and during November and December in North Carolina. Our results indicated a southerly migration route for spring-spawned juvenile bluefish that extended to northern Florida coastal waters by the end of autumn.

The disappearance of the spring-spawned cohort from the northern Florida coastal ocean after November could be the result of movement into local estuaries, offshore, or farther to the south. Morley et al. (2007) suggested that bluefish may move to the warmer waters of the gulfstream to overwinter. We recorded nearshore ocean temperatures consistently above 20˚C during November and December. It is well known that spring-spawned juvenile bluefish use MAB estuaries extensively during the summer and early fall (Juanes et al. 1996; Able et al. 2003) and Juanes et al. (2013) recently reported recruitment of the spring-spawned cohort to northern Florida estuaries in the same geographic region as the

present study increased from November to December, and that spring-spawned individuals dominated the cohort structure of juvenile bluefish during early winter. Concomitant with our results, it is evident that spring-spawned juvenile bluefish exhibit limited use of the northern Florida coastal ocean and move into local estuaries shortly after arriving to this region.

Summer-spawned juvenile bluefish selection for inner continental shelf habitats during the summer and fall in the MAB has been well documented (Able et al. 2003; Taylor et al. 2007). However, we provided a unique account of summer-spawned juvenile bluefish overwintering in the coastal ocean of the southern SAB. The summer-spawned cohort recruited to the region approximately two months after the arrival of the spring-spawned bluefish. Moreover, all but one of the juvenile bluefish collected in December belonged to the summer-spawned cohort, and this cohort continued to dominate juvenile bluefish catches in January. Summer-spawned juvenile bluefish have been shown to inhabit a narrower range of temperatures (19 – 23˚C) than the spring-spawned cohort (McBride et al. 1995). In the present study, the mean monthly ocean temperature in January was 20˚C and regional NOAA buoy hydrographic data revealed that ocean temperatures declined in February before warming again in March. Temperatures as low as 19˚C are not lethal to summer-spawned juvenile bluefish (Morley et al. 2007), but temperatures this low may have prompted summer-spawned fish to emigrate from the study area by March as only 2 individuals were collected in this month.

In January, the third cohort of juvenile bluefish began recruiting to the region in low abundance, but by March, CPE was high for these fall-spawned fish. The appearance of fall-spawned fish in this region suggests that the recruitment dynamics of juvenile bluefish may be more complicated than previously described. The contribution of the fall-spawned cohort to the adult stock structure has been considered insignificant (Wuenschel et al. 2012), but its occurrence along the U.S. coast is unique when compared to bluefish spawning in other global regions (Juanes et al. 1996). Wuenschel et al. (2012) collected early stage juveniles in the SAB during late fall to early winter and suggested that this cohort may be the result of fall-spawning during the southerly migration to overwintering waters or after arrival to the SAB, and Shepherd et al. (2006) suggested that Florida maintains a resident bluefish population. Murt and Juanes (2009) collected small (< 50 mm FL) juveniles from the surfzone along northern Florida beaches in December indicating that these fish might be the result of local bluefish spawning. Our results showed that the fall-spawned cohort was abundant in the Florida nearshore ocean from winter to early spring and may contribute locally to the bluefish stock structure, especially if Florida has a resident bluefish population. Moreover, the increased abundance of this cohort in early spring observed in the present study indicates that a substantial proportion of fall-spawned bluefish survive the winter when the risk to mortality is greatest. The contribution of the fall-spawned cohort to stock structure, especially in the SAB, should be the focus of future juvenile bluefish recruitment investigations.

3.4.4 Diet composition

This study represents the first description of the feeding behavior of juvenile bluefish inhabiting inner continental shelf waters during winter at the southern extent of the species U.S. range. Small schooling fishes were the dominant prey of juvenile bluefish collected from northern Florida coastal ocean. Juvenile bluefish fed entirely on pelagic prey, approximately 95% of which were fishes. Of the pelagic fishes found in juvenile bluefish stomachs, striped anchovy dominated the diets throughout winter in this region, and the primary importance of striped anchovy to juvenile bluefish has not been reported elsewhere. Although engraulids have contributed strongly to the prey base of juvenile bluefish in more northern waters (Juanes et al. 1993; Buckel and Conover 1997; Scharf et al. 2004; Gartland et al. 2006), bay anchovy (*Anchoa mitchilli*) was the dominant engraulid found in bluefish stomachs. A possible explanation for the importance of striped anchovy to juvenile bluefish winter foraging we observed was the habitat sampled in this study. Past examinations of juvenile bluefish feeding habits have mainly occurred in estuaries and surfzones, whereas the present study sampled bluefish by trawling the ocean in depths from 5 – 18 m. We collected few bay anchovy in the coastal ocean while this species was abundant in the associated inshore estuaries (Juanes et al. 2013). The differential habitat use exhibited by the 2 engraulids may explain the species contributions to juvenile bluefish diets observed along the northern Florida coastal ocean whereby bay anchovy may have selected for estuarine and surfzone habitats and striped anchovy selected for coastal shelf waters. Able et al. (2010) collected striped anchovy exclusively in coastal ocean waters during the summer and fall along the N.J. coast were, while bay anchovy occurred in both estuarine and open ocean habitats. In a South

Carolina estuary, 36% of the fish community was comprised of bay anchovy while striped anchovy contributed only 2.7% in relative abundance and these 2 species exhibited opposite correlations between an inlet and creek shorezone habitats (Ogburn-Mathews and Allen 1993). In the current study bay anchovy contributed only 0.5% to the total fish catch whereas striped anchovy represented the second most abundant species collected.

Five taxa were present in juvenile bluefish stomachs, and striped anchovy was the only prey positively selected throughout winter in this region. No crustaceans were consumed and Ommastrephidae (squid) represented the lone invertebrate prey, suggesting that bluefish consumed a relatively abundant but species-limited prey base. Further, the negative selection for the most abundant prey species (Atlantic bumper) and complete avoidance of other potential prey species of similar lengths as those consumed by juvenile bluefish contrasts with observations in MAB waters where bluefish displayed a more generalist feeding strategy (Friedland et al. 1988; Juanes et al. 1994; Juanes and Conover 1995; Buckel et al. 1999a; Harding and Mann 2001; Gartland et al. 2006;). Five of the 9 most abundant potential prey species were completely avoided by juvenile bluefish. All of these prey groups were small pelagic schooling fishes, as were those consumed by bluefish. Four of the 5 fishes (lookdown, moonfish, Atlantic butterfish, and harvestfish) avoided by juvenile bluefish are considered deep bodied species. These prey species were deemed available to juvenile bluefish based on body length, but body depths weren't recorded during this study. Juvenile bluefish may have avoided these species due to mouth gape limitations. Nonetheless, the contribution of striped anchovy, complete

avoidance of crustaceans and modest importance of squid observed in the present study represents a unique feeding behavior for this species.

Unlike other studies that have showed a positive relationship between juvenile bluefish size and prey size (Juanes et al. 1993; Buckel et al. 1999b; Scharf et al. 2004), we found no such relationship. The lack of a positive relationship between predator and prey size appeared to be due to the narrow range of striped anchovy sizes consumed over all bluefish sizes. Juvenile bluefish consumed striped anchovy sizes ranging from 45 – 79 mm TL, but striped anchovy as large as 126 mm TL were collected from the sample area. Further, the mean relative prey size of 25% indicated that juvenile bluefish were selecting for smaller prey. Selecting small prey is consistent with past observations of juvenile bluefish predator-prey size relationships (Juanes et al. 2002; Scharf et al. 2003), and may be associated with the increased benefits to feeding rates as a result of reduced handling time.

3.4.5 Feeding intensity

Temperature plays an important role in regulating consumption rate in fishes (Hurst 2007). As a result, many temperate species endure a period of reduced or suspended feeding during winter. Pangle et al. (2004) reported that the amount of food consumed had an influence on winter survival, with fed fishes more likely to survive than starved individuals. Although the frequency of empty bluefish stomachs (46%) observed during winter in the present study was higher than reported in other regions during the summer and early fall (Juanes et al. 1993; Hartman and Brandt 1995; Gartland et al. 2006), our

results indicated that juvenile bluefish did not suspend feeding during winter in this region. In addition, only 26% of juvenile bluefish had empty stomachs during winter in northern Florida estuaries (Juanes et al. 2013). Finally, in this study, stomach fullness was higher in March than in December and January indicating that northern Florida waters provided juvenile bluefish with the physical and biological environment for continued feeding during winter.

The low frequency of empty stomachs and high stomach fullness in the morning suggests juvenile bluefish feeding may be more intense near dawn in northern Florida waters. This early diurnal foraging behavior has been observed in juvenile bluefish feeding in mid-Atlantic estuaries, where bluefish fed at higher rates during the crepuscular periods (Juanes and Conover 1994; Buckel and Conover 1997). Spatially, juvenile bluefish had higher stomach fullness values in the shallow strata than in deeper waters. It is well known that bluefish is a highly mobile species (Shepherd et al. 2006) and could quickly move between the shallow and deep strata in the study area. Consequently, juvenile bluefish collected with full stomachs from the shallow strata may not have been the result of feeding exclusively in depths less than 10 m. However, catch rates of striped anchovy were more than 2 times greater in shallow transects than in the deep strata, and this disparity in prey depth associations could be related to the increased feeding intensity observed for juvenile bluefish inhabiting the shallow strata.

The diet composition was similar but the feeding intensity varied among the 3 juvenile bluefish cohorts during winter in the northern Florida coastal ocean. To our knowledge,

this study represented the first diet content description for fall-spawned juvenile bluefish. The frequency of empty stomachs was similar between the spring- and summer-spawned cohorts and considerably lower than the fall-spawned cohort. It was unlikely that this cohort-specific variability in empty stomachs was the result of interactions among the cohorts due to the observed migration patterns whereby little temporal overlap occurred among the cohorts throughout the study period. Instead, the differences in the frequency of empty stomachs observed among the cohorts could be due to the monthly variability in striped anchovy abundance. Striped anchovy abundance was lowest in March when the fall-spawned cohort dominated juvenile bluefish catches.

3.4.6 Lipid content

As water temperatures decline during winter, the feeding rates of temperate fishes typically decline and lipids are mobilized to meet physiological requirements (Cunjak et al. 1987; Hurst et al. 2000). For juvenile bluefish residing in the northern SAB during winter, the mobilization of lipids resulted in a reduction of lipid storage across almost all body depots including white muscle tissue (Morley et al. 2007; Slater et al. 2007). Conversely, we found a general increasing trend in the lipid content of juvenile bluefish inhabiting the northern Florida coastal ocean through the winter. Similarly, Juanes et al. (2013) showed that age-0 and age-1+ bluefish collected from northern Florida estuaries also accumulated lipids from fall through winter. The contrasting autumn lipid content in fish from these two regions is likely associated with the seasonal north-south migration strategy exhibited by juvenile bluefish along the U.S. east coast (Weunschel et al. 2012). Juvenile bluefish were shown to store energy in the northern SAB during the fall in

90

preparation for the southerly migration (Morley et al. 2007). However, fish subjected to prolonged northern SAB winter water temperatures, simulating overwinter residency in the northern SAB region, depleted their lipid levels during the winter (Slater et al. 2007). Our results indicate that fish which move to the southern SAB in the fall exhaust lipid stores during the migration and arrive to the overwintering region with low lipid content. The subsequent increase in lipid content we observed during December and January was likely the result of optimal water temperatures for juvenile bluefish feeding and abundant prey resources in our sample area.

We were unable to disentangle the seasonal versus cohort energy dynamics of juvenile bluefish because each monthly lipid content assessment represented an individual cohort. However, we provided a unique account of cohort-specific juvenile bluefish overwintering energetics, such that the lipid content was greatest in the summer-spawned cohort. Juanes et al. (2013) reported a modest relationship between bluefish size and lipid content during the winter for spring-spawned individuals. In the present study, spring-spawned juvenile bluefish were larger than fish from the other two cohorts, but the lipid content was lowest for this cohort. A possible explanation for this disparity in energetics could be that spring-spawned bluefish exhausted energy storage during the southward migration and replenished lipid content after moving into northern Florida estuaries as was reported by Juanes et al. (2013). Moreover, Slater et al. (2007) showed that unfed spring-spawned juvenile bluefish depleted lipid stores more rapidly than summer-spawned fish. Summer-spawned bluefish could have conceivably compensated

91

for lower size-related lipid reserves prior to the winter migration if they were able to store

lipids more rapidly or efficiently than spring-spawned fish during winter.

Table 3.1. Temporal and spatial trends in catch-per-effort (CPE) within and among the spring-, summer- and fall-spawned cohorts of juvenile bluefish. The fish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08. Significant differences in CPE by row are indicated with a letter superscript and by column with a number superscript.

| | Cohort | | |
	Spring	Summer	Fall
Month			
October	0.44^{a1}	-----	-----
November	1.31^{a1}	-----	-----
December	-----	2.86^{a1}	-----
January	-----	27.94^{a2}	0.11^{b1}
March	-----	0.13^{a3}	4.56^{b2}
Site			
St. Augustine (1)	0.19^{a1}	1.19^{b1}	-----
Matanzas (2)	0.13^{a1}	6.61^{b2}	0.39^{a1}
Flagler (3)	0.22^{a1}	19.93^{b2}	1.85^{c3}
Ponce (4)	0.56^{a2}	12.52^{b2}	0.56^{a12}
Depth			
Deep	0.36^{a1}	13.66^{b1}	0.39^{a1}
Shallow	0.17^{a1}	5.20^{b2}	1.00^{c2}
Time			
Morning	0.33^{a1}	5.35^{b1}	0.32^{a1}
Afternoon	0.23^{a1}	16.70^{b2}	1.25^{c2}
Evening	-----	0.10^{a3}	-----

Table 3.2. Diet composition of juvenile bluefish. The fish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08. The frequency of occurrence (FO) was based on the number of stomachs with prey, the percent composition by wet weight (W) was expressed as the total weight of that taxon divided by the total stomach content weight, and the percent composition by number (N) was expressed as the number of individuals of that taxon divided by the total number of prey.

		2006/07			2007/08		
		FO	W	N	FO	W	N
2006/07							
Total stomachs examined, N	278						
Total containing prey, n	127						
2007/08							
Total stomachs examined, N	156						
Total containing prey, n	106						
Vertebrata							
Engraulidae							
Anchoa hepsetus		47	68	61	83	86	90
Clupeidae							
Opisthonema oglinum		3	5	3	--	--	--
Carangidae							
Chloroscombrus chrysurus		--	--	--	2	6	2
Trichiuridae							
Trichiurus lepturus		1	1	1	5	3	2
Unidentified fish remains		43	21	29	9	3	4
Invertebrata							
Ommastrephidae							
Illex sp.		5	5	4	1	2	1

Table 3.3. The percentage of empty stomachs in juvenile bluefish. The fish were collected from the northern Florida coastal ocean arranged by year, month, time period, station and cohort. The percent empty stomachs for month, time period, station and cohort were combined across years.

| Parameter	Percent empty stomachs
Year	
2006/07	77.7
2007/08	35.6
Month	
October	50.0
December	40.0
January	60.0
March	82.5
Time period	
Morning	45.0
Afternoon	81.3
Site	
St. Augustine (1)	30.0
Matanzas (2)	70.0
Flagler (3)	88.0
Ponce de Leon (4)	46.1
Cohort	
Spring	50.0
Summer	59.6
Fall	84.8
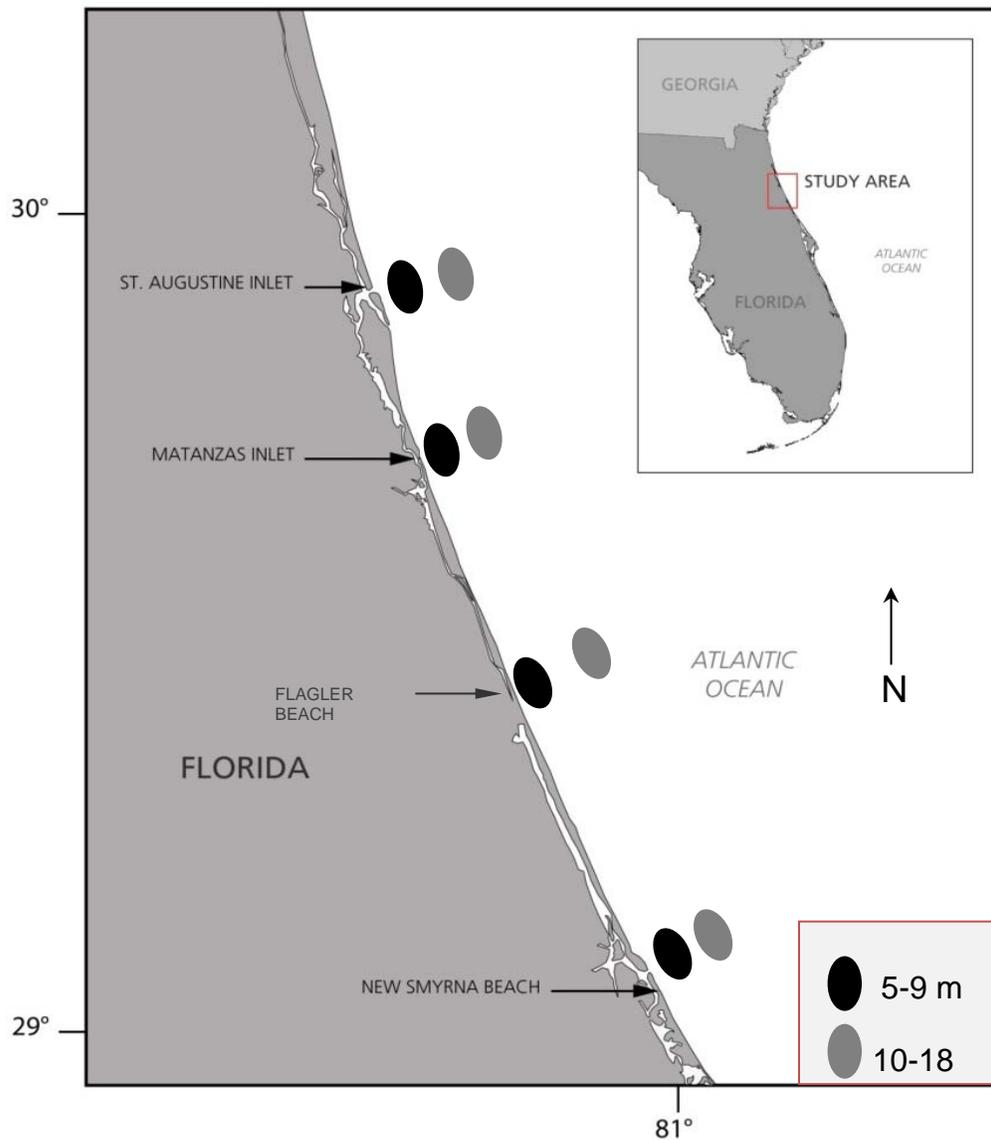
Figure 3.1. Map of the study area showing the locations of the four sites off the coast of northern Florida. The sites were sampled during winter 2006/07 and 2007/08. Black ovals represent the areas encompassing the shallow (5-9 m) transects and gray ovals represent the areas encompassing the deep transects (10 – 18 m).
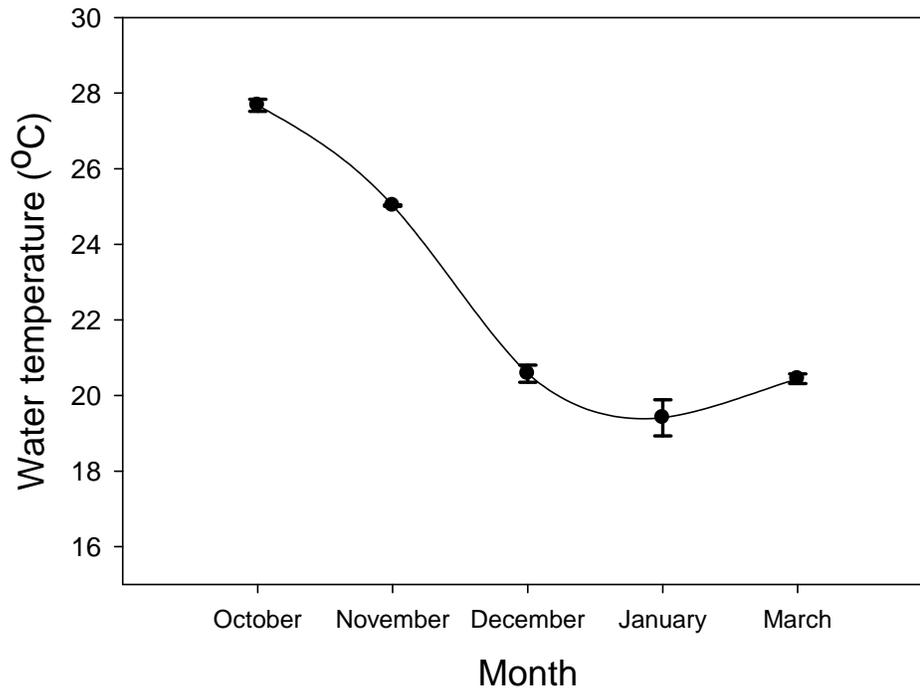
Figure 3.2. Water temperature profile of the northern Florida coastal ocean study area. The average monthly ocean temperatures (± between year standard error) are combined for the study years 2006/07-2007/08. February is omitted because no sampling took place during this month.
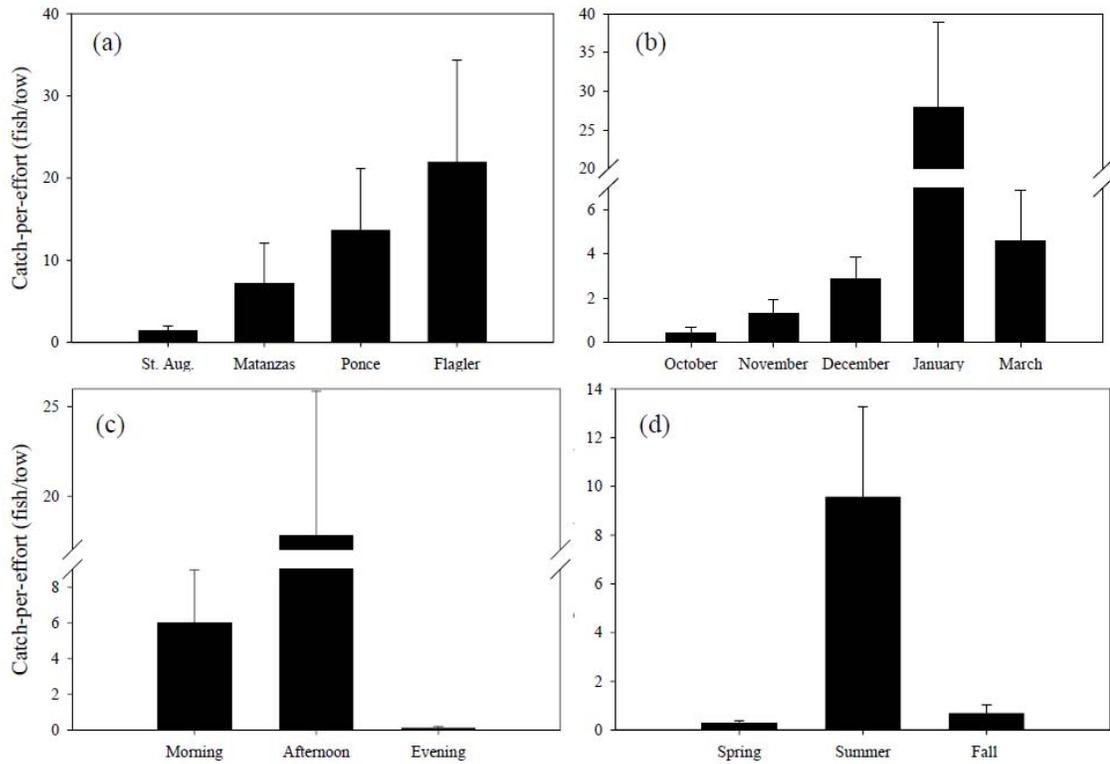
Figure 3.3. Catch-per-effort (CPE) of juvenile bluefish. The fish were collected from the northern Florida coastal ocean and combined for 2006/07 and 2007/08. The four panels represent the CPE by (a), site; (b), month; (c), time period; (d), cohort. Note the differences in the scales of CPE. Error bars denote the standard error in CPE.
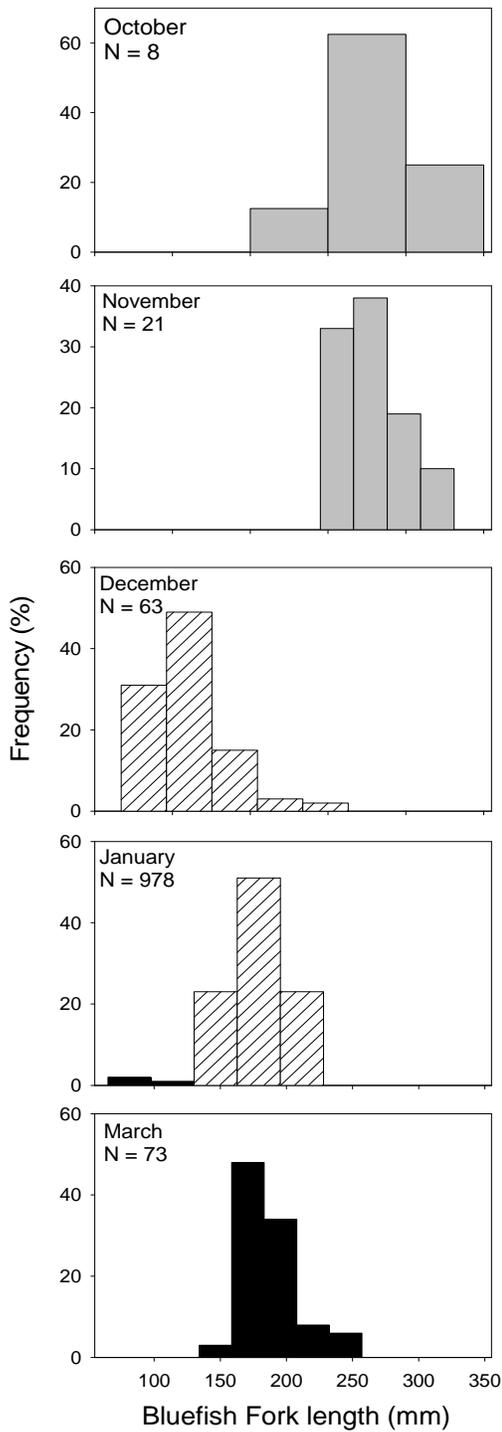
Figure 3.4. Monthly length frequency distributions of juvenile bluefish. Fish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08 (combined across years). Gray bars represent the spring-spawned cohort, hatched white bars represent the summer-spawned cohort and black bars represent the fall-spawned cohort.
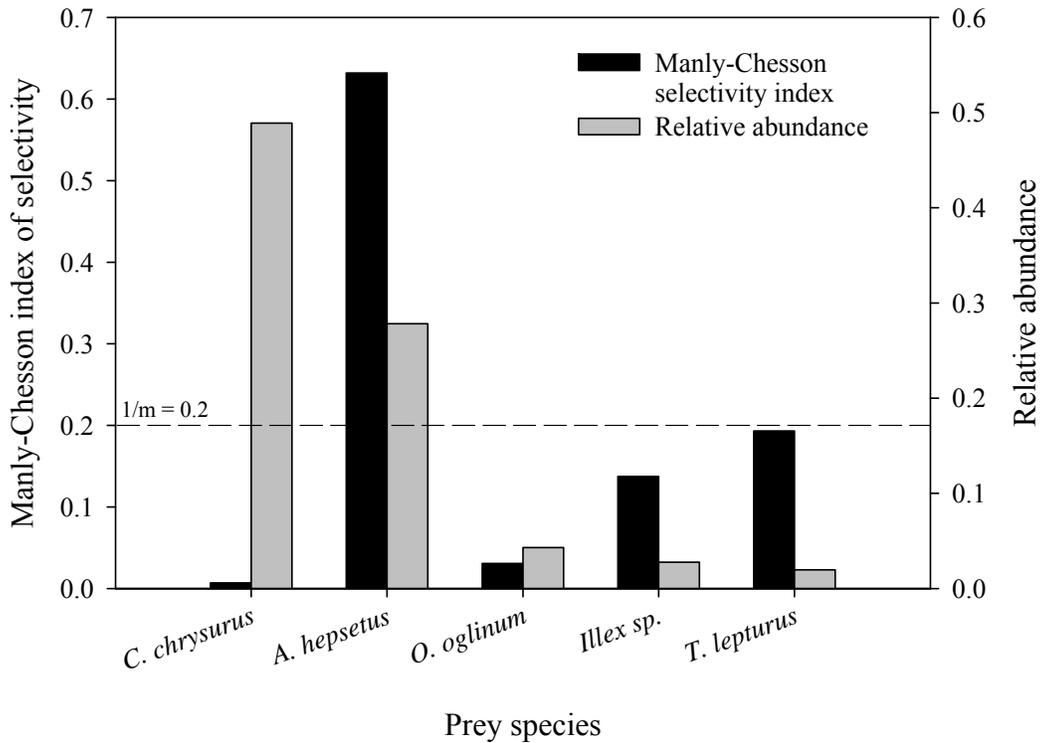
Figure 3.5. Manly-Chesson index of selectivity and relative abundance of the 5 prey groups consumed by juvenile bluefish. The fish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08 (data have been combined across years). For each prey group, a Manly-Chesson index value above the dashed line indicated positive selection and a value below the dashed line indicated negative selection. The prey were ordered along the x-axis from greatest to least relative abundance.
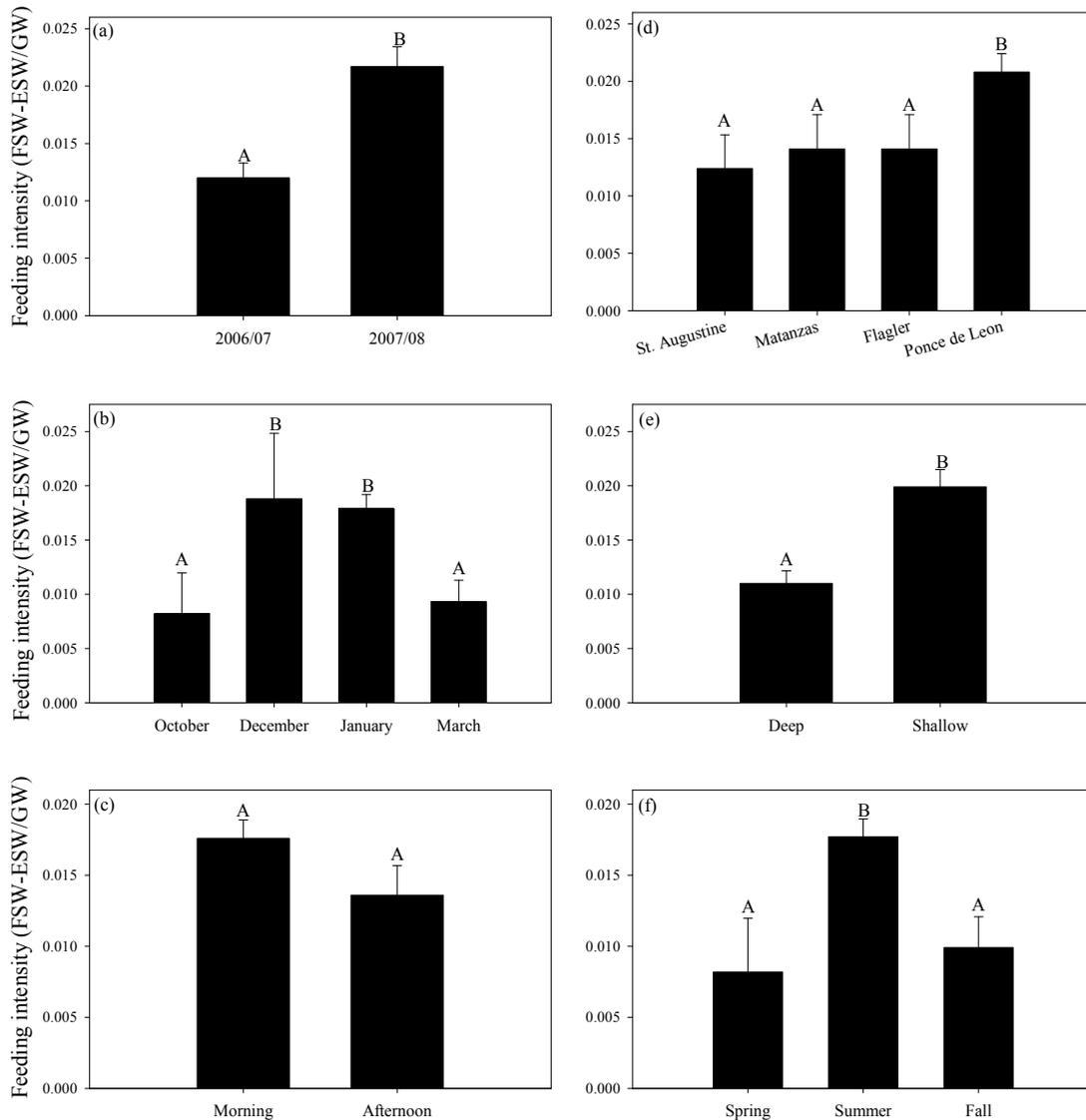
Figure 3.6. Feeding intensity of juvenile bluefish. The fish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08. The panels represent juvenile bluefish feeding intensity by (a), year; (b), month; (c), daily time period; (d), sampling station; (e), depth stratum; (f), cohort. No interaction in feeding intensity of juvenile bluefish was observed between year and month, daily time period, sampling station, depth, stratum or cohort, so years were combined. Error bars represent standard error. Within each panel, error bars with different letters indicate significant differences between variables.
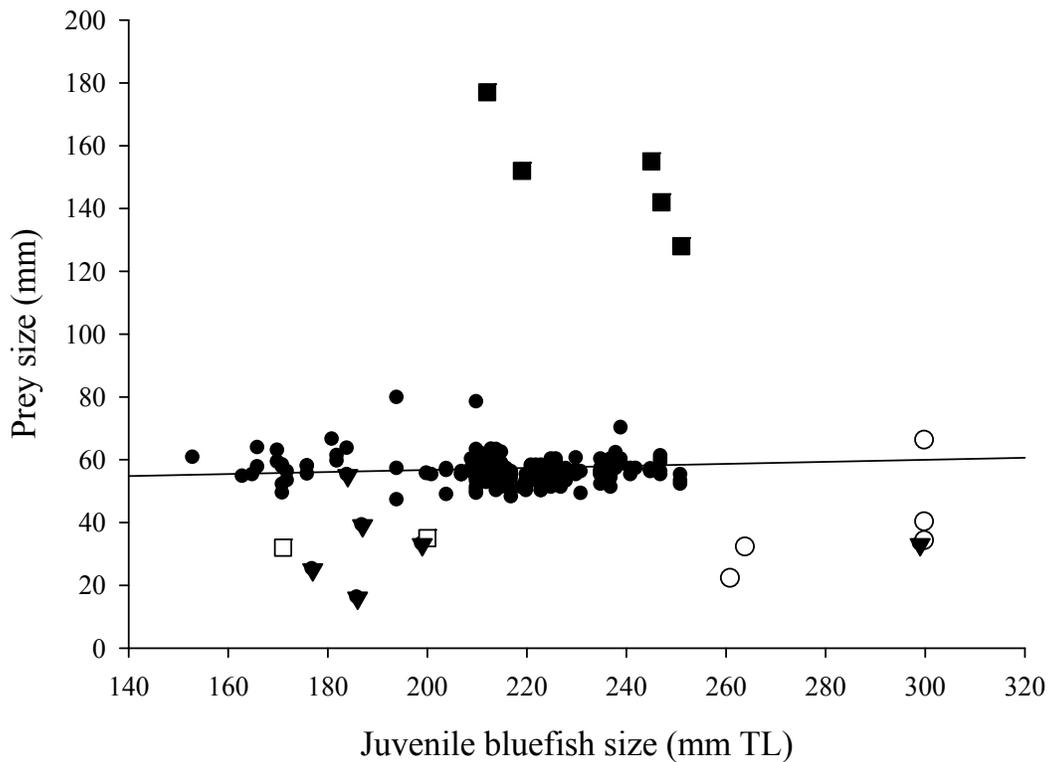
Figure 3.7. Relationship between juvenile bluefish size and the sizes of the prey consumed by juvenile bluefish. The fish were collected from the northern Florida coastal ocean in 2006/07 and 2007/08 (combined across years). Individual prey were identified to species except for the genus *Illex* and represented with a ● = Striped anchovy (*Anchoa hepsetus*), ○ = Atlantic bumper (*Chloroscombrus chrysurus*), □ = Atlantic thread herring (*Opisthonema oglinum*), ▼ = shortfin squid (*Illex sp.*), and ■ = Atlantic Cutlassfish (*Trichiurus lepturus*). Prey sizes (mm) were measured to total length (TL) for fishes and mantle length (ML) for squids.
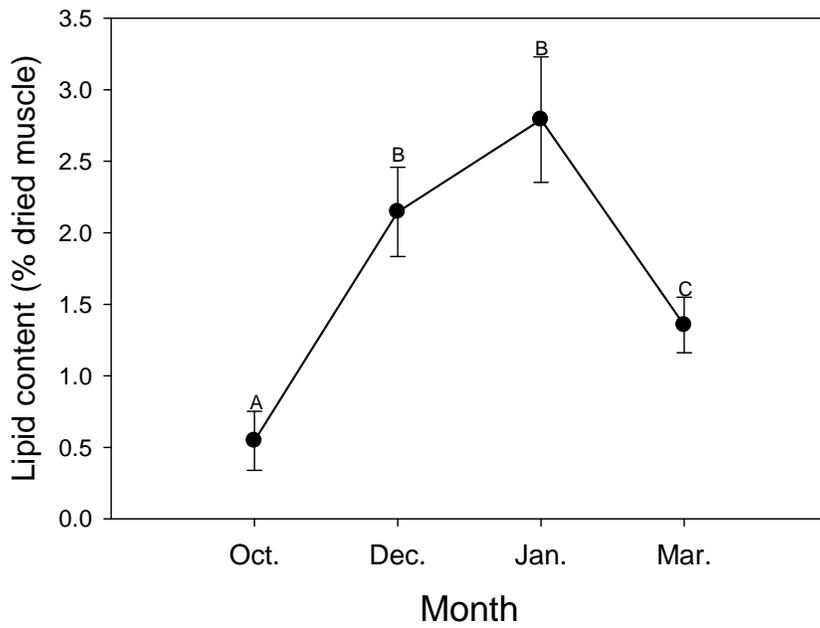
Figure 3.8. Monthly lipid content in white muscle of juvenile bluefish. The fish were collected from the northern Florida coastal ocean. Error bars represent standard error. Error bars with different letters indicate significant differences in lipid content.

CHAPTER 4

**GENERAL CONCLUSIONS ON THE REGIONAL RECRUITMENT DYNAMICS**

AND SEASONAL ECOLOGY OF JUVENILE BLUEFISH

4.1 Cohort structure

The hatch-date distributions of mid-April and late June to early July indicated that the juvenile bluefish inhabiting the lower HRE were produced from two primary spawning events in the spring and summer respectively. I found that these spring- and summer-spawned juvenile bluefish inhabited the lower HRE during the summer and early autumn of 2008 and 2009. Although the enumeration of daily growth increments on the otoliths of the juvenile bluefish collected from the northern Florida coastal ocean was not possible, length frequency analysis showed that three cohorts inhabited this region from late autumn to early spring in 2007 and 2008. In January, the third (fall-spawned) cohort of juvenile bluefish arrived to the coastal waters of northern Florida and was the only cohort still residing in these waters in March. The appearance of fall-spawned fish in this region suggests that the recruitment dynamics of juvenile bluefish may be more complicated than previously described.

While spring- and summer-spawned juvenile bluefish traded cohort supremacy between years in the lower HRE, the summer-spawned cohort dominated the cohort structure in the northern Florida coastal ocean during both years of the Florida study. These results corroborated the hypothesis that a shift has occurred in the cohort structure favoring the summer-spawned cohort over the last several years. Although I cannot conclude that the

juvenile bluefish spending the summer and early autumn in the lower HRE migrate all the way to the northern coastal waters of Florida, the high relative abundance of summer-spawned fish in the region during winter suggests that many members of this cohort survive the autumn migration. My results also corroborated the existence of a third cohort of juvenile bluefish and these fall-spawned fish should be included in future recruitment indices.

4.2 Spatial and temporal recruitment dynamics

Overall, the water temperatures in the lower HRE from July to October and along the northern Florida coast from late October to March were within the preferred range for juvenile bluefish and corroborated the belief that broad-scale juvenile bluefish migrations are associated with local seasonal water temperatures. My results showed that juvenile bluefish overwinter in southern SAB areas with similar water temperatures in the MAB prior to the autumn migrations. Moreover, December could represent a transitional period in the seasonal migration of juvenile bluefish such that inter-annual water temperatures during this month in the SAB oscillated around 14°C in northern regions, but were consistently above the minimum temperature tolerance of juvenile bluefish in the southern SAB. Finally, it has been suggested that juvenile bluefish may migrate to the warmer offshore waters of the Gulfstream to overwinter. However, my results showed that juvenile bluefish overwintered in the northern Florida coastal ocean, indicating that a southward migration likely explained the movement of juvenile bluefish away from MAB waters to the southern SAB during the coldest months of the year.

From a regional perspective, the earlier hatch-dates of spring-spawned juvenile bluefish clearly resulted in at least a two-week earlier arrival to the lower HRE than the summer-spawned cohort. The factors responsible for the timing of juvenile bluefish egress from the HRE are less clear. Although the water temperature of the lower HRE began to decline in September of 2008 and 2009, the temperature remained above 15°C through October. However, both cohorts had disappeared from the estuary by the end of this month in both years. Moreover, the autumn water temperatures differed between years, but in an unpredictable way relative to juvenile bluefish emigration timing. The production cycle of bay anchovy, the primary prey of juvenile bluefish in the lower HRE, differed considerably between years in a manner more consistent with the emigration timing of juvenile bluefish suggesting that the out-migration of juvenile bluefish from this nursery area was more closely aligned with the timing of prey production than water temperature.

Similar to the migration dynamics that I observed for bluefish in the lower HRE, spring-spawned juvenile bluefish arrived to the northern Florida coastal ocean approximately two weeks to one month earlier than their younger conspecifics in both years of the study. The spring-spawned cohort was also larger than summer-spawned fish, both upon egress from the lower HRE and arrival to northern Florida in the two years of the two studies. The differential phenology and size distributions between the two cohorts in the two regions were consistent across years, suggesting that the near one month lag in the arrival of summer-spawned fish to its overwintering areas could be the result of the earlier emigration timing and size-related faster swim speeds of the spring-spawned cohort.

Similar to what I found regarding the prey production cycle in the lower HRE, the ocean temperatures in March along the northern Florida coast were well within the preferred juvenile bluefish range, but the spring- and summer-spawned cohorts had left the area. Further, the CPE of the preferred prey (striped anchovy) of juvenile bluefish in this region was the lowest of the study period during this month, suggesting that the regional water temperature was a strong indicator for the ingress of juvenile bluefish to their seasonal nursery areas, but the emigration timing was primarily attributed to the local prey production cycle.

Finally, previous investigations of the temporal recruitment dynamics of juvenile bluefish in the MAB and northern SAB have concentrated on the timeframe ranging from summer through autumn and found that maximum bluefish abundance correlated with decreasing latitude over this temporal scale. My study represented the first examination of juvenile bluefish recruitment dynamics during the winter, in which the regional abundance of bluefish was greatest during January.

4.3 Feeding behavior

Although the diet composition of juvenile bluefish has been described throughout most of the species U.S. range, I presented the first description of the feeding behavior of juvenile bluefish inhabiting inner continental shelf waters during winter at the southern extent of its distribution in the northwest Atlantic Ocean. To my knowledge, this study also represented the first diet content description for fall-spawned juvenile bluefish throughout

the species range, and the primary importance of striped anchovy to juvenile bluefish inhabiting coastal ocean waters has not been reported elsewhere.

A novel discovery of my project was the similarity in prey type between spring-spawned and summer-spawned juvenile bluefish in the lower HRE, and among all three cohorts in the northern Florida coastal ocean, in that both cohorts consumed almost exclusively bay anchovy in the lower HRE and striped anchovy in the northern Florida coastal ocean. Juvenile bluefish have been shown to be generalist predators in other regions, but I found that all of the cohorts selected for a single species of prey within each region and season, indicating that juvenile bluefish may be adopting an alternative feeding strategy. The causes of such a change in the feeding behavior should be the focus of future research. Moreover, the importance of these closely related forage fishes to the diet of juvenile bluefish over the scale of 1000+ km is remarkable from an ecological perspective, but should also be included in future bluefish management plans.

4.4 Growth and energetics

I found that spring-spawned juvenile bluefish were larger than the summer-spawned cohort by the time of emigration from the lower HRE in both years irrespective of the cohort-specific growth rate. Although a comparison of growth was not an objective of chapter three, length frequency analysis showed that the spring-spawned cohort was also considerably larger upon arrival to the northern Florida coastal ocean in October than summer-spawned bluefish during the winter. Moreover, although summer-spawned bluefish exhibited positive growth during the winter in this region, they were still smaller

by the time they emigrated from the study area in January than spring-spawned fish three months earlier, indicating that the spring-spawned cohort maintains its size advantage over the summer-spawned cohort throughout the first year recruitment period.

To my knowledge, this study represented the first assessment of the lipid content in juvenile bluefish inhabiting MAB waters during the summer prior to the autumn migration and after migrating to the southern SAB coastal ocean during winter. Due to the sampling protocol in the lower HRE, I was unable to make any conclusions about spring-spawned juvenile bluefish arrival energetics, but combined with the results of the lipid content analysis of juvenile bluefish arriving to the northern Florida coastal ocean, it is reasonable to conclude that the summer-spawned bluefish incurred a modest energy deficit during transport to the summer seasonal nursery area, while the spring-spawned cohort exhausted almost all its energy reserves during the autumn migration to the northern Florida coastal ocean. Furthermore, the consistently lower lipid content of juvenile bluefish combined across cohorts during winter than summer confirms the importance for juvenile bluefish to find adequate resources prior to the autumn migration.

For most juvenile fish inhabiting temperate waters during the summer and early autumn, recruitment success may depend on individuals selecting for maximum growth over energy accumulation during the growing season to avoid size-selective natural mortality and to survive their first winter when growth is typically nil. The inverse trend in lipid content between spring- and summer-spawned juvenile bluefish in the lower HRE from summer to early autumn in both years of the study and largest difference in lipid content

between the summer- and spring-spawned cohorts occurring at the end of the summer indicated that lipid content may not be as size-dependent as previously assumed and that a cohort-specific physiological tradeoff or constraint between growth and energy utilization exists in juvenile bluefish. Finally, the 2009 study season in the lower HRE provided a unique opportunity to assess the influence of energetics of juvenile bluefish on migratory behavior. In this year, the feeding intensity of both cohorts was consistent during early autumn, but a subsequent rapid decline in lipid content October may have triggered juvenile bluefish to begin their southerly migration.

4.5 A final thought

For fishes that spawn within a discrete time period and produce a single cohort of offspring, recruitment success may be determined by the presence or absence of a single stochastic environmental event, resulting in either a good or bad year-class. The spawning behavior of bluefish which results in multiple cohorts of young may dampen recruitment variability by spreading the mortality risk out over time and space. It has been well established that the lower HRE acts as a nursery area for multiple cohorts of juvenile bluefish to maximize growth potential during the summer and early autumn. I showed that juvenile bluefish also utilize this estuarine nursery to store energy in preparation for the long migration to their overwintering habitats. Perhaps most importantly, I revealed the way in which the two cohorts partitioned the estuary to reduce the competitive bottleneck. In a large estuary like the HRE, the spring- and summer-spawned cohorts avoided intra-specific inter-cohort competition by separating their niches in the spatial dimension and fed on different age-classes of bay anchovy. This

niche separation widened or eliminated the juvenile competitive bottleneck, such that summer-spawned fish did not appear to suffer any negative consequences to occupying different habitats than their older conspecifics during the first summer of life.

I found that the northern Florida coastal ocean shelf functions similar during winter to surf zones and estuaries during the summer and autumn in providing abundant resources and appropriate temperature for continued bluefish growth as well as energy accumulation for the return migration in the spring to MAB waters. The temperature in the nearshore oceanic waters of northern Florida were warmer than associated estuaries and above the lower thermal tolerance of juvenile bluefish, making the northern Florida coastal ocean a thermal refuge for juvenile bluefish during the winter. I showed that although spring-spawned juvenile bluefish exhibit limited use of coastal ocean waters, the summer-and fall-spawned cohorts of juvenile bluefish utilized this habitat extensively throughout the winter and this area should be considered essential juvenile bluefish overwintering habitat.

In contrast to the mechanism by which the inter-cohort competition was reduced in the HRE, the three cohorts partitioned the use of the northern Florida coastal ocean over a temporal scale from October and November (spring-spawned cohort) to December and January (summer-spawned cohort) to March (fall-spawned cohort). Remarkably, almost no temporal overlap occurred among the three cohorts during the study. In summary, the consistently low bluefish recruitment estimates over the past several years may be the

result of reduced spawning potential from the long-term below-target adult biomass

levels instead of a reduction in juvenile survival.

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